Density, movements and hunting of feral cats in relation to fire and grazing in northern Australia

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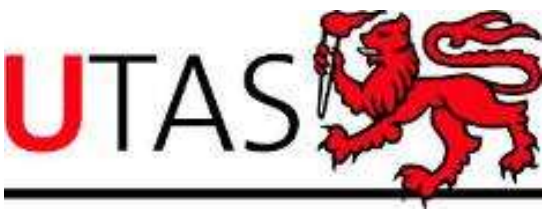

Declarations

This thesis contains no material which has been accepted for a degree or diploma by the University or any other institution, except by way of background information and duly acknowledged in the thesis, and to the best of the m y knowledge and belief no material previously published or written by another person except where due acknowledgement is made in the text of the thesis, nor does the thesis contain any material that infringes copyright.

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Data collection fulfilled all legal requirements in Australia, and has been approved by University of Tasmania Animal Ethics Committee (A0011661) and Western Australian Department of Parks and Wildlife Animal Ethics Committee (2010/35), with a Western Australian Government Regulation 17 licence to research animals (SF009379). All research was conducted with permission on three pastoral leases: Mornington Wildlife Sanctuary, Marion Downs, and Glenroy Station.
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Abstract

Vegetation structure plays a pivotal role in predator-prey interactions, because it influences the effectiveness with which predators are able to detect, pursue or ambush their prey, and determines the opportunities for prey to avoid being exposed to predators. Therefore, changes in vegetation structure may alter the impacts of predation on populations of prey species.

In recent decades, populations of small mammals have collapsed across much of the savannah biome of northern Australia. The causes of this decline are not known, but predation by feral cats, intensification of fire regimes, and intensified grazing by introduced herbivores have all been implicated as possible causes by correlative and circumstantial evidence. However, we do not understand the mechanisms by which these factors, alone or in combination, affect population size in small mammals. Without this mechanistic understanding it is difficult to prescribe management interventions that will protect small mammals from further declines and allow recovery.

I investigated interactions between predation by feral cats and vegetation structure in a study area in the central Kimberley region of northwestern Australia, to test whether one effect of fire and grazing regimes is to amplify the impacts on small mammals of predation by feral cats. I addressed three specific objectives. First, I measured population density of cats differed in areas with contrasting fire and grazing regimes. The second objective was to test how the movements of individual cats were influenced by vegetation and habitat structure, and especially to show whether cats preferentially hunted in burnt or grazed areas. The third objective was to derive direct measures of kill rates of feral cats, to show how these were influenced by habitat characteristics.

To determine cat density, I deployed six arrays of infrared cameras across the study area during 2012 and 2013. The arrays were allocated evenly to areas with and without large introduced herbivores, and ranged across areas with differing fire histories. Each array consisted of 15 or more cameras deployed for one month. All cats ‘captured’ on camera were individually identified, and density was estimated using spatially-explicit mark-recapture

analyses. Density at all six arrays was generally similar (mean 0.18 cats per km^2, with SE of 0.08). There was no significant difference in density between grazed and un-grazed arrays, despite a five-fold difference in small mammal abundance. These results demonstrate that cats occur at low density in the Kimberley compared to other parts of Australia, and that population density does not increase when small-mammal abundance increases in ungrazed areas.

To investigate movement behaviour and fine-scale habitat selection by cats, I deployed GPS collars on 32 cats in landscapes with contrasting fire and grazing treatments, and used discrete-choice modelling in relation to detailed habitat measures to reveal the movement decisions that underlie habitat selection by individual cats. Cats selected areas with more open grass cover, heavily grazed areas, and areas close to standing water. Mild fire scars were avoided, but cats strongly selected for areas recently burnt by intense fires in habitats with high abundance of small mammals. Not only was this the strongest influence on movement decisions made by cats within their home ranges, but cats also predictably journeyed up to 15 km to temporarily exploit areas recently burnt at high intensity outside the borders of their home range.

I deployed collar-borne video cameras on cats to record hunting events and to measure the effects of habitat on hunting success. In this way I obtained 98 hours of cat activity, during which 101 hunting events were observed. The success or failure of cats in killing prey at a hunting event was strongly affected by habitat. For hunting events in which prey were in a grass tussock or a rocky refuge, the kill rate was four times lower (18 %) than in open areas (76 %). That is, cats enjoyed higher hunting success in the habitat types that they preferred to enter.

This research demonstrates how a relatively sparse population of cats can have major impacts on prey populations if disturbance regimes are not managed appropriately. In particular, cats respond well to the conditions created by intense fire and grazing, increase their hunting in such areas, and accomplish higher hunting success. Vegetation structure is pivotal to creating ideal landscapes for predators to hunt, or conversely, to providing refuges for prey to avoid predation. Intense fires are likely to become more prevalent with climate change, and this could increase the impacts of many species of small to medium sized predators. A useful

broad principle to reduce the impacts of this predation could be to increase the spatial and temporal cover of ground vegetation wherever possible.

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CHAPTER 1

General introduction

Era of global extinctions

We are currently experiencing the highest rate of extinction of animal species in Earths' history, outside of very large meteor impacts (Dirzo *et al.* 2014). At least 320 animal species have gone extinct in the last 500 years, and around 20 % of all extant vertebrate species are considered at risk of extinction (IUCN 2014). The primary reason for this sudden pulse of extinctions is that the massive expansion of human populations and impacts has caused a vast diversity of changes to ecosystems throughout the world, over a very short timeframe in ecological terms (Dirzo *et al.* 2014). Specific anthropogenic changes include over-hunting, introduction of species to new ecosystems, broad-scale clearing of habitat, alteration of disturbance regimes (e.g. fires), and climate change (Pimm *et al.* 2014). Most species are now subjected to multiple threats, such that overcoming or adapting to one may not be sufficient for survival. Often, these threats operate synergistically in ways that amplify their impacts (Brook *et al.* 2008). All these changes are operating at a pace that is, for the most part, too swift to allow species to adapt to the changed conditions and so persist.

Mammalian extinctions in Australia

The fauna of Australia has suffered an especially severe extinction rate. Australia has had a comparatively long geographic isolation from any other continent, and evolved a unique fauna as a result. However, since 1500 AD Australia has lost more mammal species than any other continent. These extinctions occurred after European settlement, from 1850 to 1950 (Johnson 2006).

The dominant cause of mammalian extinctions in Australia was the introduction of exotic predators, the red fox *Vulpes vulpes* and the feral cat *Felis catus* (Woinarski *et al.* 2014). Other factors such as hunting, vegetation clearing and competition with rabbits have contributed to the declines of mammals, but their impacts have not been as profound (Burbidge and McKenzie 1989; Johnson 2006; Smith and Quin 1996) and cannot explain the complete extirpation of formerly widespread species. Different landscapes across Australia were affected to differing degrees. South-eastern Australia and the arid and semi-arid regions were especially hard hit, losing almost all their terrestrial small to medium sized mammals (50 g to 4,400 g). Many species also declined and went extinct in eastern and south-western Australia (Burbidge and McKenzie 1989). Some species went extinct soon after European expansion into inland Australia (Johnson 2006), whilst others lingered at low densities until the 1960s (Burbidge *et al.* 1988), when indigenous people left the land. In contrast, the fauna of Australia's northern monsoon tropics was largely spared, with only a small subset of mammals being lost (Cramb and Hocknull 2010; Start *et al.* 2012). This was possibly due to the absence of the red fox, and the lack of broadscale land clearing in northern Australia. Even as late as the 1980s, mammal surveys were still capturing largely intact mammal assemblages in the north (e.g. Churchill 1997; Dunlop and Begg 1981).

Declines of mammals in northern Australia

Our picture of an intact mammal fauna across northern Australia has recently changed, as there have been population declines of all small to medium sized terrestrial mammals recorded in the last 20 years (Woinarski *et al.* 2011a). This includes dramatic crashes of abundance and diversity of small mammals in seemingly intact ecosystems, such as Kakadu and Litchfield National Park (Woinarski *et al.* 2010, see Figure 1). Similar declines have been reported elsewhere across northern Australia (Woinarski *et al.* 2011a). The cause (or causes) of these declines remains elusive, and no single factor adequately explains them. Critically, these drivers must be understood in order to implement effective conservation (Woinarski *et al.* 2014) .

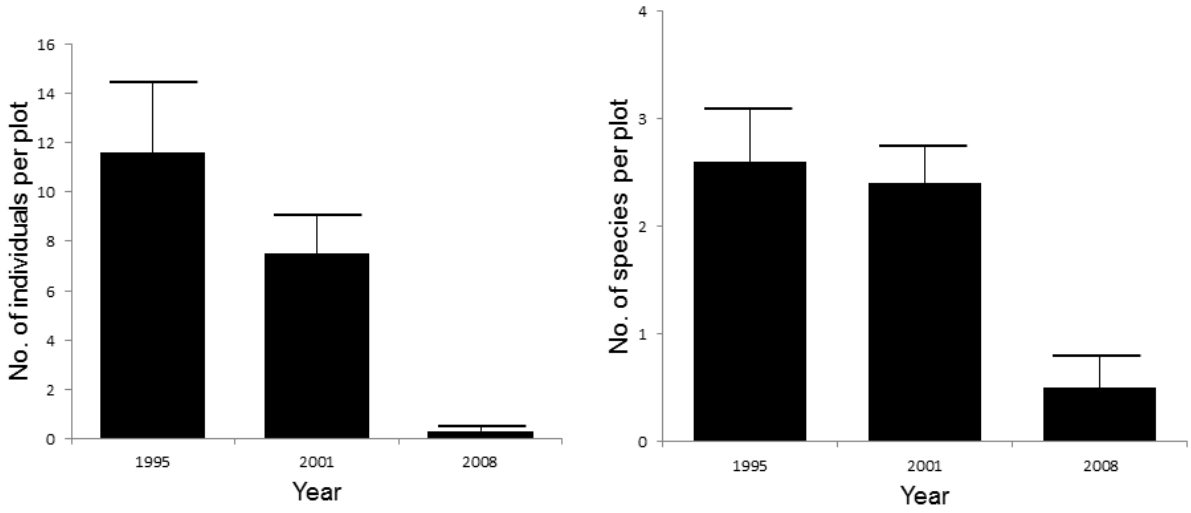

Figure 1. Change over time in Kakadu National Park at 15 plots of the number of individual mammals trapped (left) and species richness per plot (right). Columns show the mean and standard error (reproduced from Woinarski *et al*. 2010).

There is evidence that predation by feral cats is at least in part responsible for this decline of small mammals. This is suggested by three lines of evidence. First, populations of mammals in complex rocky habitats have been less affected than those in more productive woodlands and savannas. Complex rocky topography would provide additional shelter from predation, yet no extra food for most species, suggesting that top-down impacts are driving the declines (Oakwood 2000; Radford *et al.* 2014). Second, the declining species fall within the preferred prey-size range of cats (Dickman 1996; Fisher *et al.* 2013). Finally, populations of declining mammal species are more stable in the absence of cats, on islands or in large enclosures (Frank *et al.* 2014; Woinarski *et al.* 2011b). However, the declines cannot be attributed solely to the introduction of cats. There is a temporal mismatch between the arrival of cats in northern Australia (up to 170 ya in some places; Abbott 2002) and declines of mammals observed in the last 50 to 20 years (Woinarski *et al.* 2011a).

Other environmental factors have changed over the last 50 to 20 years. Fire regimes have changed substantially, shifting from frequent small-scale fires lit by indigenous Australians (Hall *et al.* 2009), to large-scale uncontrolled wildfires that burn more extensively, are more intense, and consume a higher proportion of vegetation (Russell-Smith *et al.* 2003). An example of how fire patterns have changed is presented in Figure 2 below, which shows how indigenous burning created a mosaic of small-scale fire scars, a pattern that broke down once

indigenous people left the landscape. Similar patterns are well documented elsewhere across northern Australia.

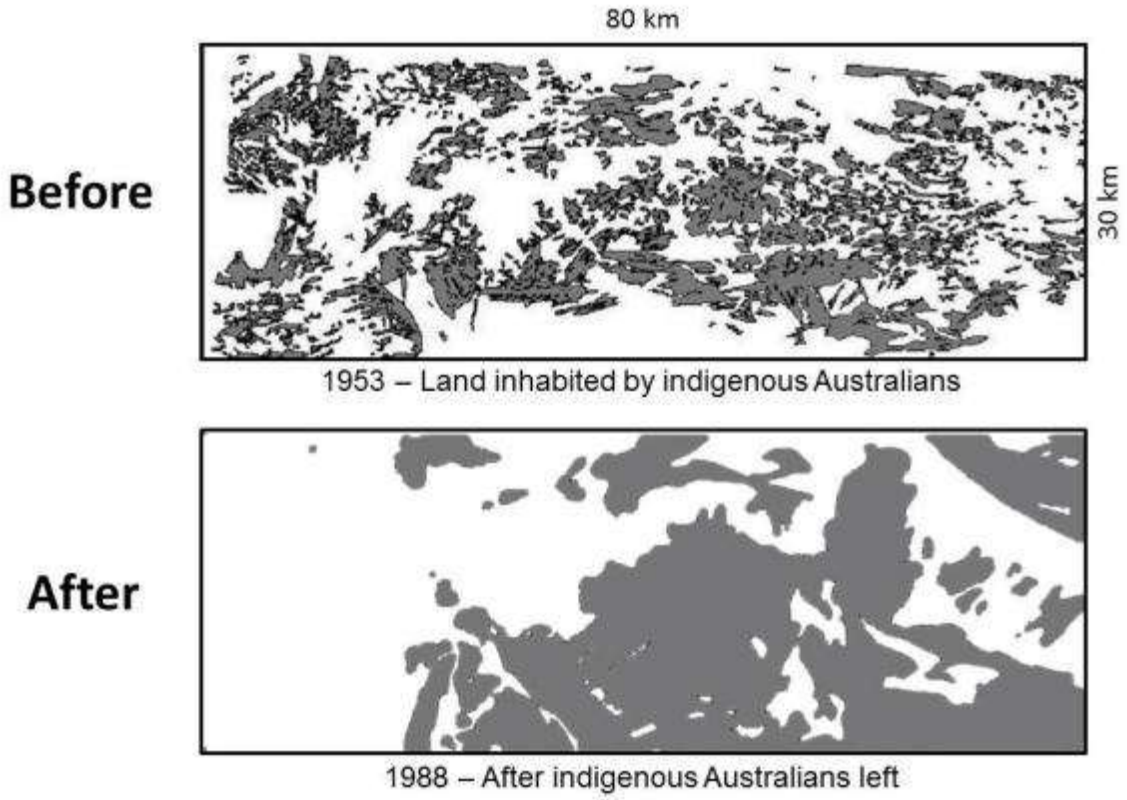

Figure 2. Fire patterns (grey) inferred from aerial photographs in the Great Sandy Deserts from 1953, when indigenous Australians, the Pintupi people, still inhabited the landscape, compared to fire patterns in 1988 after the area was vacated (reproduced from Burrows *et al.* 2004).

Grazing by large feral herbivores has also have increased in some areas over recent decades, although the extent of change is unlikely to be as pronounced as for fire regimes. The first settlers brought cattle *Bos taurus* and horses *Equus caballus*, and by the 1900s much of northern Australia supported herds of domestic or feral herbivores. Densities of large introduced herbivores may have increased in certain areas, as cattle species more adept to the north-Australian climate were introduced (*Bos indicus*) to replace the original *Bos taurus* stock which was less resilient to hot and dry conditions. Populations of other large feral herbivores, such as feral horses, donkeys *Equus asinus* and buffalo *Bubalus bubalis*, may have increased as well. Also, intensification of pastoralism is likely to have increased the size of managed herds, in turn increasing grazing pressures.

In general, small mammals show greater declines in areas where fires are larger and more intense (Andersen *et al.* 2005; Kutt and Woinarski 2007; Legge *et al.* 2008), and where the impact of grazing is greatest (Kutt and Woinarski 2007; Legge *et al.* 2011; Woinarski and Ash 2002). However, as for cats, the patterns and magnitude of decline cannot be solely attributed to fire and grazing regime changes. Intense fires are not always detrimental to populations of small mammals. Studies on Marchinbar and Melville Island have both reported that fire events appear to be beneficial for declining native mammals (Davies and Murphy 2014; Southgate *et al.* 1996). Also, declines have continued even in areas where large herbivore populations have probably decreased, such as Kakadu National Park (Woinarski *et al.* 2010). Thus neither cat predation, intensification of fires, nor increased grazing pressure explain the declines in northern mammals alone. However, it is possible that all these mechanisms are operating in concert.

The following hypothesis has been put forward to explain the recent mammal declines: that the impacts of cat predation become greater when it interact with certain fire and grazing regimes (Johnson 2006; Woinarski *et al.* 2011a; Ziembicki *et al.* 2013). This could explain the apparent mismatch in timing between the arrival of cats and these declines, along with inconsistencies of the impacts of fire and grazing regimes. Reduction of structural complexity of vegetation and increased openness due to fire and grazing might increase the exposure of small mammals to predators, making prey easier to detect and capture. Small mammals are cats' preferred prey (Dickman 1996; Kutt 2012). If cats preferentially use the open and relatively simple habitats created by fire and grazing, the result could be higher predation impacts on small mammals. This has been suggested as a possible mechanism for these declines (Johnson 2006; Woinarski *et al.* 2011a; Ziembicki *et al.* 2013), however, there is currently no evidence that can be used to test whether this mechanism is operating, and whether its effects are powerful enough to explain the observed declines of small mammals.

There is strong basis for this hypothesis in ecological theory. Fire and grazing regimes shape vegetation structure, which plays a major role in predator hunting success (e.g. Hebblewhite *et al.* 2005). Low vegetative cover (less than 1 m high) is especially important for most small to medium sized terrestrial vertebrates, as it comprises the bulk of biomass at their height, and contains the dominant food sources for them or their prey. Vegetation at this height is also especially susceptible to changes in disturbance regimes, even at very small temporal

scales. Such changes ultimately affect the overall abundance of prey in habitats with different fire and grazing regimes, which in turn can alter the populations and movement decisions of prey (Sinclair *et al.* 1998).

Low vegetation can also affect the process of actual hunting events. Many animals require cover to either hide from predators or stalk and ambush prey, while others depend on open vegetation structure to allow vigilance for predators. Also, complex vegetation can provide a medium in which one species is able to move at a speed and/or tortuosity that the other cannot. The impact of this is especially pronounced where there is a large discrepancy between the size of the predator and the size of the prey, as the smaller animals may be able to move quickly through dense and complex vegetation while the larger are impeded. For this reason, vegetation structure is likely to be of greatest importance to prey populations when predators are larger than their prey, and may be less so if predator and prey are either similarly sized or prey are larger. In such cases more species-specific factors such as locomotor skills and capacity to mount a defence would become more important (Orsdol 1984). With such a wide variety of potential interactions, the manner in which vegetation affects hunting events depends on the predator, prey and ecological context.

Given these considerations, there are numerous mechanisms by which intensification of fire and grazing regimes could increase predation rates imposed by feral cats. Fire and grazing might reduce habitat suitability for some small mammals, which could in turn reduce recruitment to a threshold at which cat predation becomes overwhelming. Such changes may also alter the movement patterns of cats, so they are more likely to hunt in burnt or grazed habitats. Hunting by feral cats could be enhanced, as small animals become easier to hunt. Cats have one of the largest ratios between their own size and that of their prey of any carnivore, approximately 1:0.03 (Kitchener 1991; Vézina 1985), so it is likely that their prey can move quickly through complex low vegetation (e.g. spinifex tussocks) while they cannot. Therefore, if changes in fire and grazing regimes were to reduce the spatial and temporal cover of vegetation, then their predatory impacts may be greater.

Aims

The aims of this thesis were to test the hypothesis that predation impacts of feral cats are more pronounced under intensifying fire and grazing regimes, to an extent that could explain

recent declines in the north-Australian mammal fauna. This was achieved by analysing cat impacts at different scales in monsoon savanna landscapes with contrasting fire and grazing patterns in the central Kimberley region of Western Australia. First, I measured population densities of feral cats at six sites with contrasting fire and grazing regimes, to determine if population density responded to the differences in vegetation caused by fire and grazing. Second, I assessed fine-scale movements of feral cats, to test whether individual cats preferentially hunted in burnt or grazed areas within their home ranges. Third, I assessed large-scale movements of feral cats to determine whether they would travel outside of their home ranges to hunt in such areas. Fourth, I used animal-borne video cameras to observe the hunting of feral cats to determine whether open or grassed habitats either increased or decreased their success rate. Finally, I assessed all this together in context, to provide a synthesis of evidence bearing on the hypothesis, and to estimate the magnitude of the impacts of the hypothesised process on populations of small mammals.

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Thesis structure

Each chapter of the thesis is written as a separate article for publication in a different journal, so there is some repetition of background material and description of study areas to establish the context for each paper. Formatting remained consistent between chapters, however, this will be altered for publication. For all chapters, I am the lead author. My supervisors were co-authors on all papers. For chapter 2, Joanne Potts is a co-author as she provided the design and framework for the data analysis.

Chapter 2 - Density and home range of feral cats in north-western Australia.
This has been submitted to Wildlife Research, and is awaiting decision.

Chapter 3 - Landscape management of fire and grazing regimes alters the fine-scale habitat utilisation by feral cats.
This has been accepted in PlosOne, and will be published online soon.

Chapter 4 - Long-distance hunting expeditions to intense fire scars by feral cats.
This has been prepared for submission in Nature Communications. As this paper draws heavily on the previous two chapters, I am awaiting their acceptance for publication before I submit this.

Chapter 5 - Hunting behaviour of feral cats in a tropical savannah, revealed by animal-borne video-collars.
This has been prepared for submission in Journal of Applied Ecology. Before submission, I shall alter the figures to be in greyscale.

Photos of study area and methods

A short photo essay is presented below to facilitate an understanding of the landscapes this study was undertaken in, and the methods involved.

Typical habitat of the study area, with a dense grass understorey and open eucalyptus woodland interspersed with boab trees.

Fires are a major feature of the landscape. Early in the year, fires are small in scale and trickle through the landscape (photo by Katherine Tuft)

Late in the dry season, fires can be very large scale and intense.

Cat detection dogs ready to spotlight for cats, Sally on the left and Brangul on the right (photo by Wayne Lawler)

Sally leading a chase to retrieve a GPS collar from a cat, with Toby Barton, Danni Lisle and Hugh McGregor (photo by Wayne Lawler)

Feral cat captured and fitted with a GPS collar, about to be released.

Tracking feral cats from part of the King Leopold range.

CHAPTER 2

Density and home range of feral cats in north-western Australia

Hugh McGregor, Joanne Potts, Sarah Legge, Menna Jones, and Chris N. Johnson.

Published in: *Wildlife Research*

Feral cat detected on infrared camera with *Rattus tunneyi*

Abstract

Context. Feral cats *Felis catus* pose a significant threat to biodiversity in Australia, and are implicated in current declines of small mammals in the savannas of northern Australia. Basic information on population density and ranging behaviour is essential to understand and manage threats from feral cats.

Aims. In this study, we provide robust estimates of density and home range of feral cats in the central Kimberley region of north-western Australia, and we test whether population density is affected by livestock grazing, small-mammal abundance and other environmental factors.

Methods. Densities were measured at six transects sampled between 2011 and 2013 using arrays of infrared cameras. Cats were individually identified, and densities estimated using spatially explicit capture-recapture analysis. Home range was measured from GPS tracking of 32 cats.

Key results. Densities were similar across all transects and deployments, with a mean of 0.18 cats per km^2 (range 0.09 km^{-2} to 0.34 km^{-2}). We found no evidence that population density was related to livestock grazing or small-mammal abundance. Male home ranges were on average 855 ha (95 % CI ± 156 ha, n = 25), and females were half the size at 397 ha (95 % CI ± 275 ha, n = 7). There was little overlap in ranges of cats of the same sex.

Conclusions. Compared to elsewhere in Australia outside of semi-arid regions, feral cats occur at low density and have large home ranges in the central Kimberley. However, other evidence shows that despite this low density, cats are contributing to declines of small mammal populations across northern Australia.

Implications. It will be very difficult to reduce these already-sparse populations by direct control. Instead, land management practices that reduce the impacts of cats on prey should be investigated.

Introduction

Feral cats *Felis catus* are a major threat to biodiversity conservation in Australia (Dickman 1996) and the primary threat to many extant mammals (Woinarski *et al.* 2014). While there are numerous examples of cats causing localised population declines and extirpations of prey species (Christensen 1980; Fancourt 2014; Risbey *et al.* 1999), little is known about the full extent of their impacts, especially compared to less cryptic introduced mammals like foxes *Vulpes vulpes.* Quantifying the potential impacts of feral cats, and devising management strategies to reduce those impacts, requires information on population density and ecology of feral cats. Such information is generally not available in many habitats and regions across Australia.

Acquiring density estimates for cats in Australia is difficult, as cats are challenging to capture and detect (Short *et al.* 2003). They are typically solitary, cryptic, and display little interest in bait. To date, cats have mostly been monitored using passive activity indices (Kennedy *et al.* 2012; Lazenby and Dickman 2013; Read and Bowen 2001). While such measures may capture changes in relative abundance at local scales, they do not provide estimates of absolute abundance. In a few instances, abundance has been estimated from spotlight counts in the arid zone (e.g. Read and Bowen 2001; Short and Turner 2005) and the temperate south-east (see Denny and Dickman 2010 for full list; Jones and Coman 1982). However, the wary nature of cats means that they are likely to have low detectability by spotlight counting, and sighting transects are therefore likely to underestimate true abundance (Mahon *et al.* 1998; Read and Eldridge 2010). Bengsen *et al.* (2012) estimated cat densities outside of townships on Kangaroo Island to be 0.7 km^{-2}, but this was an area without sympatric foxes or dingoes *Canis familiaris dingo*, so is unlikely to be representative of mainland Australia. In tropical Australia, basic information on density and home range remains unknown. Understanding the density and home range of feral cats is important to interpreting their full impacts in these ecosystems.

Currently, cats appear to be threatening many native mammals in tropical Australia (Woinarski *et al.* 2011a; Woinarski *et al.* 2014). Feral cats are the only introduced mesopredator in tropical Australia, and across most of the north they have no similar-sized native counterpart. Most species of terrestrial small mammals in this region have been

declining, and there is evidence that this is due, at least in part, to predation by feral cats (Fisher *et al.* 2013; Frank *et al.* 2014; Woinarski *et al.* 2011b). However, all available evidence suggests that densities of cats in the north are low. Indices from track counts on sandpads have recorded cat tracks on between 0.06 % and 22 % of pads per night (Catling *et al.* 1999; Ibbett 2010; Kennedy *et al.* 2012), which is generally lower than elsewhere in Australia. Spotlight surveys in Kakadu National Park at different areas suggested densities of 0.7 km^{-2}, 0.2 km^{-2} (Ibbett 2010) and 0.03 km^{-2} (Braithwaite *et al.* 1984, in Ibbett 2010). These low estimates could either reflect genuinely low abundance, or an abundant yet cryptic population. Both interpretations have vastly different implications for how the impacts of feral cats could be managed.

Densities of feral cats are likely to vary between habitat types and management regimes. In particular, we expect density to increase with small-mammal abundance, as this predicts activity elsewhere in Australia (Short and Turner 2005). Density may also vary with water availability, as wetter areas may have greater concentrations of prey and potentially higher densities of cats (Braithwaite and Griffiths 1994). Different management regimes may also alter cat densities, as grazing by domestic stock would open up the ground layer, potentially improving hunting effectiveness. Declines of native mammals are strongest in areas with intense grazing pressure by introduced herbivores (Legge *et al.* 2011a), raising the question of whether cat densities are also higher in such areas.

Home range and spacing of individuals are important considerations for the impacts of feral cats on prey, along with helping to devise effective management strategies. As density estimates generally have large confidence intervals, variations in densities at finer spatial scales can be inferred from measuring home range size (Liberg *et al.* 2000). In this study, we provide the first robust estimate of density and home range size of feral cats in north Australia. Density was estimated using spatially explicitly capture-recapture analysis (Borchers and Efford 2008), from data gathered by motion-triggered infrared cameras to uniquely identify cats. This method can provide density estimates with an appropriate spatial reference, unlike traditional mark-recapture analysis. To determine the spatial distribution of cats, we compared cat density between areas with different riparian habitat characteristics and grazing by feral herbivores. We did not consider effects of fire as there was insufficient variation at a landscape scale to compare between transects, however, such impacts are

considered at a finer scale (Chapter 3). Finally, since we were limited by the sample-size of landscape-scale density estimates, we investigated habitats likely to affect cat density at a smaller spatial scale by analysing variations in their home range size using GPS collars. Smaller home ranges generally indicate a greater localised density (Barratt 1997; Wolff 1985), so smaller home ranges for feral cats, relative to their size and sex, should be linked to higher cat densities.

Methods

Study area

Our study area was in the central Kimberley of northern Western Australia (17°01'S, 126°01'E), spread over three pastoral leases (see Figure 1). One is managed as a working pastoral station (Glenroy; 1455 km^2), and the other two are wildlife sanctuaries managed by the Australian Wildlife Conservatory (Mornington, 3130 km^2; and Marion Downs, 2500 km^2). The area has a tropical monsoon climate, generally divided into three broad seasons: the wet (December – March), early dry (April – July) and late dry (August – November). All properties are grazed by cattle, except a 40 300 ha fenced area in Mornington where all large introduced herbivores (cattle, horses, donkeys) have been removed, hereafter referred to as the 'destocked zone' (Legge *et al.* 2011a). The vegetation of the study area is predominantly savanna woodlands with a perennial grass layer. The grass layer of the flatter alluvial areas is dominated by *Chrysopogon fallax*, *Dichanthium fecundum* and *Heteropogon contortus*, while the dryer rockier areas are dominated by *Sehima nervosum* and spinifex *Triodia* spp. The region is dissected by sandstone ridges with complex rocks, part of the King Leopold Ranges. At the time of the study, there had been minimal cat control, apart from opportunistic shooting of between 2 and 10 cats per year across the entire extent of Mornington and Marion Downs.

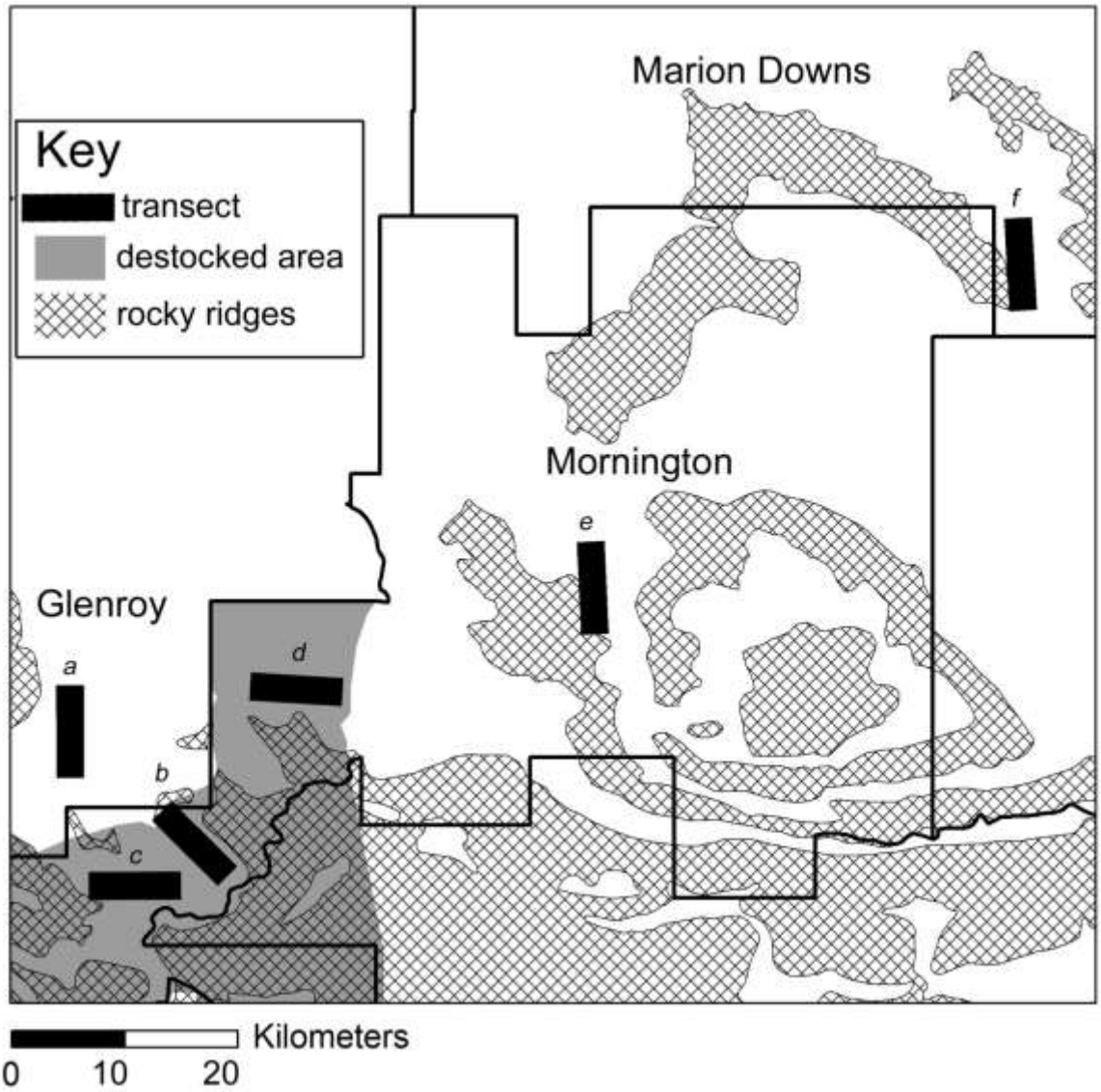

Figure 1. Map of the study area, including the six transects used to estimate cat density. This is in the central Kimberley, north-western Australia. Names of transects are *a* Annie creek, *b* Roy creek, *c* Bluebush, *d* Evergreen, *e* Bronco Valley, and *f* Marion Downs.

Camera trapping

We placed six transects across the study area (Figure 1). Three transects were in areas grazed by introduced herbivores, and three where in the destocked zone. Two transects were sampled in 2011 (Roy Creek and Annie Creek), and all transects were sampled each year in 2012 and 2013. Transects were sampled between May and September each year, and in haphazard order. Each transect was based along a road, and approximately 7.5 km long. Fifteen infrared camera traps were placed along each transect at intervals of 300 – 700 m. This spacing was chosen based on GPS tracking, showing that male cats had a maximum home range width of 3.5 km and females of 1.2 km, suggesting that all cats with a home range dissecting the transect should be able to be detected on at least two cameras (Foster and Harmsen 2012). Cameras were positioned such that probability of detection of cats would be maximised, for example by placing them on dry creek-lines and in naturally open areas. Although cats in the study area did not have strong preferences for such habitats (Chapter 3), they would typically walk along such areas for short distances if they encountered them (H. McGregor, unpublished data). Every fourth camera site had two cameras, to increase the incidence of passes where both sides of cats could be revealed. In order to keep detection probabilities as consistent as possible over the duration of each deployment, we did not use baits or lures. Cameras were deployed for between three to six weeks in each survey. Infrared cameras used were Reconyx Rapidfire Professional 600c, chosen because of their fast trigger-time (0.2 seconds). Cameras were programed to take three images per trigger, with fast shutter speed, favouring photo resolution over flash distance. They were set between 20 and 40 cm high (cat body height), facing directly into the road or creek, with the angle refined until a 'walktest' would detect our hands moving at the height of a cat along the walkway. The probability of detection was likely consistent between cameras settings, as 100 % of cat passes on paired cameras were detected by both cameras. However, it is likely cats would not be detected on any camera on warm days where ambient and cat temperatures are identical.

Each pass of a cat in front of a camera was examined in detail. Passes that did not contain sufficient information to identify cats were discarded. From all cat passes where markings were visible, the majority were tabbies (83 %), all of which had distinct markings. For each pass of a tabby without an obviously recognisable feature (e.g. a white splotch), the clearest photo of the left-flank, right flank and head (if applicable) were extracted. The patterns at key visible identifiable areas (legs, flanks and forehead) were traced in Photoshop, the trace was

saved as a separate image, and then stretched in a manner to allow consistent comparisons with other images (see Figure 2). Once all such cat passes had these traces, they were reviewed and matches made for those likely to belong to the same individual. Once all legs were linked, these were then linked to bodies and heads until all passes from each session were arranged into folders of each possible individual. Each folder was reviewed for inconsistences, and misidentified passes were reassigned. Once all folders had been reviewed by H. McGregor, the process was reiterated until a full review was made with no inconsistences (between two and four reviews per session). Then, all folders were independently reviewed by another identifier (S. Legge), at which stage there was 98 % agreement. After a final revision, we came to a complete agreement. Of the remaining black (8 %) and ginger cats (9 %), the majority (75 %, or 13 % of total) had some identifiable feature - either a mange mark, white splotch, telemetry collar, damaged ear - or were the single detection of a cat with that pelage type during the session. However, the remaining 4 % of cats could be assigned as an individual based only on a subjective assessment of head and body shape. Such cats were present in four sessions.

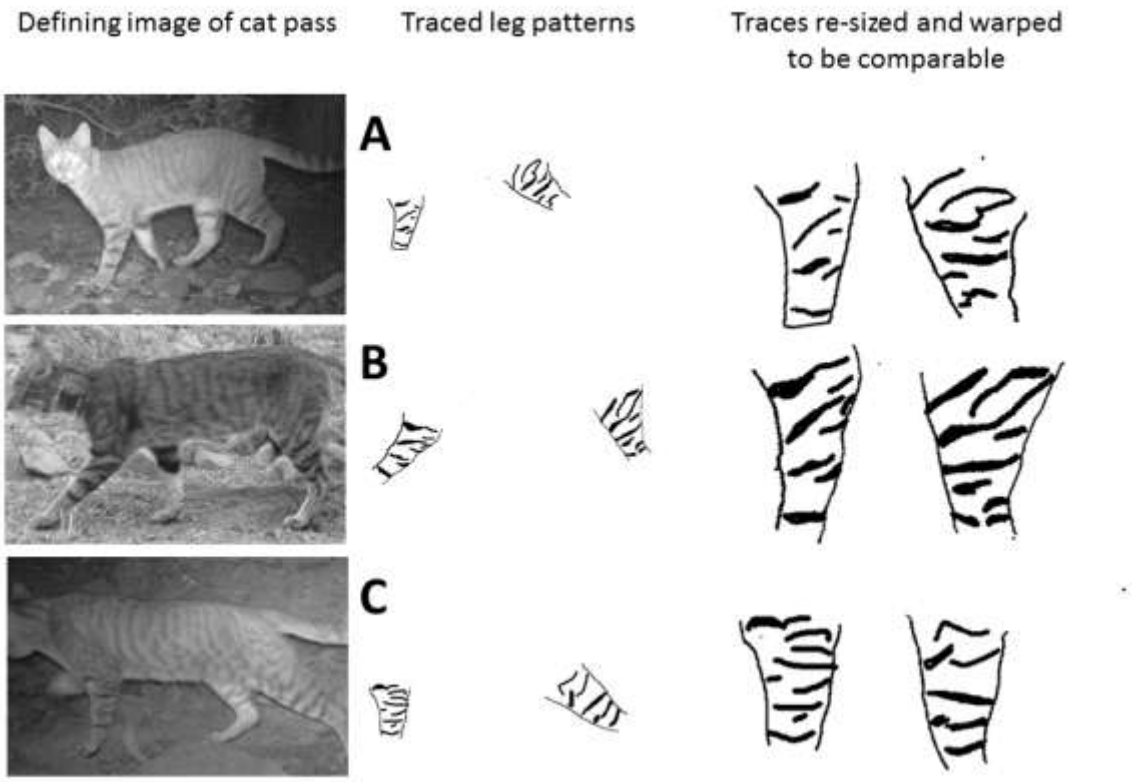

Figure 2. Examples of extracting leg-pattern shapes from photos of cats. Leg patterns are traced over in Photoshop, exported, then arranged vertically to allow easier cross-comparisons when identifying individual cats. In this example, images A and B are the same individual, while C is a different cat.

Density estimation

Encounter histories were developed for each survey session by dividing each three to six week survey period into a series of three-day intervals, in which each individual cat was scored as observed or not. Density was estimated using spatially-explicit mark-recapture analysis using the 'secr' library in R. (Borchers and Efford 2008). The spatially-explicit mark-recapture models are based on the assumption that every individual has a home range centroid on which detection probabilities are highest, and the probability of detection decreases with increasing distance from the home range centre. This method assumes home-

ranges centres to be independent, which is unlikely for cats of the same sex. However, such biases are generally evened out when access to traps is independent, i.e. locations of camera traps are not biases towards or away from home-range centres (Borchers and Efford 2008). To aid estimation of model parameters, a buffer has to be chosen as the likely maximum distance at which detection of an individual away from its home range centre is essentially zero (Balme *et al.* 2009). We chose a buffer width of consideration of 3500 m, as this is the estimated average maximum width of home ranges of male cats from simultaneous GPS data from cats.

To estimate the detection function, we first assessed which functional form (e.g., half-normal, hazard or exponential) best fit the observed data. Since cats have varied space-use patterns within their home range, all possible detection functions were considered. In these models, detection probabilities at the home range centre (referred to as 'g0'), and the shoulder of the detection function ('sigma') were constant. Models were compared using AIC values, and the detection function with the lowest AIC was used as the basis for further modelling. Next, we created a set of models with different covariates influencing 'g0' or 'sigma' (see above). They were modelled as either two unique sub-populations identified by a finite-mixture model with two classes ('h2', assuming this would capture differences between sexes), interacting with time ('t'), a learned response to cameras ('b'), and specific to the microhabitat of detectors ('g', either dry creek-bed, road or open habitat). We assessed the parameters ('g0' and 'sigma') for each model, and if the likelihood estimation process had not converged (as evidenced by standard errors being 0) the models were discarded. All model AICs were compared and from the preferred model we derived the mean density along with the lower and upper 95 % confidence intervals.

For the four sessions that contained cats subjectively identified based on shape, we ran a separate mark-resight analysis (White and Burnham 1999). Although this was not inherently relevant to a spatial scale, we compared the population estimate obtained to that of the spatially explicit capture-recapture estimate, to provide an indication for the possible scale of error considering misidentification. For this, all passes of subjectively identified cats were considered unmarked, all others marked, and detections considered for all cameras per three-day interval. The analysis was conducted in the program MARK (White and Burnham 1999).

To compare densities of cats against landscape-level factors, we used analysis of variance models with transects as error terms, compared within an information theory framework. Due to the low sample size, only two explanatory terms were used. We compared grazing regime (pastoral cattle station, or destocked conservation area), which collates strongly with small-mammal density in the study area (Legge *et al.* 2011a). We also compared the percentage of area with riparian or alluvial habitats (creeks, rivers, alluvial flats or sandseeps; see Chapter 3for details). Fire impacts were not considered, as there was little variation in fire frequency and timing between transects.

Home range estimation and interaction

Home range area and overlap were measured by capturing and GPS-collaring cats throughout the study area. Feral cats were captured between November 2010 and June 2013, using three different methods. First, large wire cage traps (30 x 30 x 90 cm; Mascot Wire Works) were used with fresh cat litter as a lure. Second, soft-jaw leg-hold traps (Victor soft-jaw size #1.5) were placed at the side of roads or dry creek-lines, surrounded in a small bower, with fresh cat-litter and a visual lure (feathers, CD, or metal tag attached 50 cm from ground with fishing line). These were checked every six hours throughout the night using telemetry trap checkers (SirTrack, New Zealand). Third, cats were located by spotlighting at night, and pursued by specially-trained dogs until they took refuge in a tree. To remove the cat from the tree, we delivered sedative (Zolotil at a rate of 0.5 c / kg) using a dart rifle (Pneu-dart X-caliber), and caught the cat in a trampoline. Once captured, cats were fitted with GPS collars (Telemetry Solutions, Quantum 4000 enhanced). Cats weighing between 2 and 3.3 kg were fitted with a 70 g collar, while those weighing more than 3.3 kg were fitted with a 100 g collar so that all collars were less than 3 % of body-weight. These GPS collars units were programmed to record one fix per day at 20:00 western standard time (+8 hrs coordinated universal time) for two days, alternating with two-day bouts in which fixes were taken every 15 minutes, starting and finishing at 12:00 noon. To replace GPS collars, cats were recaptured using the dogs.

To calculate home ranges, we used one fix per day that was either at 20:00 pm WST, or the closest acquired fix to that time from days with fixes recorded every 15 minutes. A kernel density analysis was used to define home range, using the smooth cross-validation method

and creating a shape file around the 95 % isopleth. As some cats that were studied for long periods shifted their home ranges, we needed a measure of when this shift occurred to create two or more different home range measures. Shifts were detected by measuring the cumulative home range centroid, assessing where it plateaued, then noting any subsequent sudden departure from this point. Only home range shifts are considered here, as long-distance travels will be examined in a further paper. Area in hectares was calculated for each.

Overlap of home ranges was measured for every pair of neighbouring cats in the study, defined as any two cats with 200 m or less between the boundaries of their 95 % isopleth. The percent of area overlap was measured for each male-male and male-female dyad. All analysis was conducted in R (R Development Core Team 2008) and ArcMap v. 10, using the program Geospatial Modelling Environment (Beyer 2012).

We used generalised linear models to determine whether home range size varied with landscape features or traits of individual cats. Spatial variables measured were grazing regime, percent of riparian or alluvial vegetation within the home range, and small mammal density. Morphological variables considered were cat gender, weight (average of start and end weight for duration of deployment), and age class (adult, sub-adult). The resulting 64 models were compared within an information theory framework.

Results

Population density

From the six transects and fourteen deployments of camera traps from 2012 to 2013, we obtained sufficient detections to estimate density in 13 deployments. In total, 863 cat passes were recorded and individual cats were identifiable in 820 of these, representing a total of 98 individually identified cats. These were spread over 3314 trap nights, with an average of 255 per deployment (min. 175, max 440).

Using spatially explicit capture-recapture analysis, we found cat densities to be similar across all transects and deployments (see Table 1), with a mean of 0.18 cats per km^2 (range 0.09 km^{-2} to 0.34 km^{-2}). The 95 % confidence intervals for each session were large, but constant across deployments (see Table 1). For the four sessions where one of the cats could only be subjectively identified by shape, we separately run mark-resight models considering that cat as unidentified returned similar population estimates for the same effective trapping area (Table 2), although with much smaller confidence intervals. There were no significant interactions between cat density and grazing regime (d.f. = 4, F = 0.006, P = 0.94) or percent of riparian area (d.f. = 4, F = 0.075, P = 0.78).

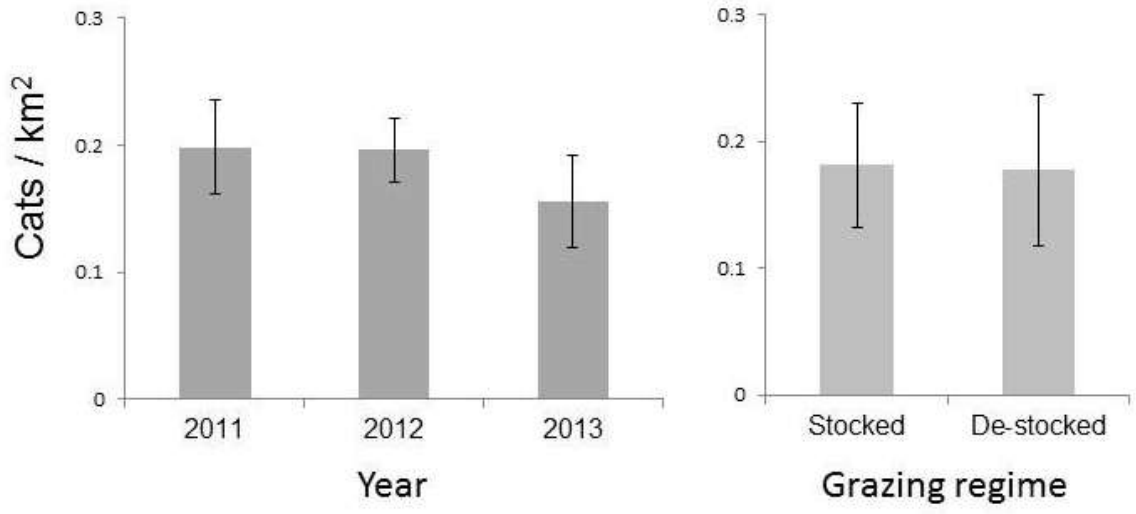

Figure 3. Differences in mean cat density per km^2 against grazing regime (left) and year of survey (right), with 95 % confidence intervals.

Table 1. Cat density measured at the six transects between 2011 and 2013. Density is from the spatially-explicit mark-recapture model with the lowest AICc value, including standard error (SE), and 95 % confidence intervals (LCI and UCI). This model's detection function is listed as either half-normal (hn), exponential (exp) or hazard-rate (hrz). The models parameters of 'g0' and 'sigma' are listed, with the chosen explanatory variables (N = null, trap = trap habitat effect), value and standard error. 'g0' is the likelihood of detection at the home range centre, sigma is shoulder of the detection function (a wide shoulder implies cats are seen at greater distances from their home range centre).

			Density				Detection	g0			sigma		
Transect	Year	Month	**Cats km^{-2}**	SE	LCI	UCI	function	g0	value	SE	sigma	value	SE
Annie Creek	2011	Aug	**0.26**	0.1	0.11	0.58	hn	trap	0.15	0.07	N	1072	225
	2012	May	**0.16**	0.06	0.08	0.31	hn	N	0.15	0.05	trap	2026	477
	2013	Apr	**0.22**	0.13	0.07	0.67	hn	trap	0.51	0.2	N	1010	292
Roy Creek	2011	Jun	**0.14**	0.06	0.06	0.33	exp	N	0.3	0.15	N	1100	438
	2012	July	**0.1**	0.04	0.05	0.21	exp	N	0.25	0.12	N	1629	596
	2013	May	**0.09**	0.03	0.04	0.19	exp	N	0.38	0.13	N	1212	267
Bluebush	2012	Sept	**0.24**	0.09	0.11	0.5	hn	N	0.32	0.07	trap	1182	207
	2013	Apr	**0.16**	0.06	0.08	0.31	hrz	N	0.32	0.05	N	2325	183
Bronco Valley	2012	May	**0.21**	0.07	0.12	0.39	hn	trap	0.46	0.18	N	1018	204
	2013	Sept	Data deficient										
Evergreen	2012	Jun	**0.33**	0.14	0.15	0.67	hn	N	0.44	0.12	N	832	126
	2013	Jun	**0.16**	0.1	0.05	0.5	hn	N	0.31	0.11	N	961	297
Marion Downs	2012	Aug	**0.13**	0.09	0.04	0.44	exp	N	0.35	0.27	N	1197	863
	2013	Jul	**0.1**	0.04	0.04	0.23	exp	N	0.12	0.14	N	723	514
Mean values			**0.18**	**0.07**	**0.08**	**0.41**			**0.31**	**0.12**		**1253**	**361**

Table 2. For the four sessions where one of the cats could only be subjectively identified by shape (e.g. black cat with no mark), the spatial-explicit mark-recapture population estimates (SECR) for the effective trapping area (Area km^2) are compared to a mark-resight model using the same data, except with subjectively identified cats considered as un-identified. LCI and UCI are 95 % lower and upper confidence intervals.

		Area	SECR output			Mark-resight output		
Transect	Year	km^2	**N**	LCI	UCI	**N**	LCI	UCI
Annie Creek	2011	74	**16.3**	7	38.3	**16.8**	15.4	18.6
Annie Creek	2012	77	**12.3**	6.1	22.7	**10.7**	9.8	12.8
Roy Creek	2013	88	**7.9**	3.2	13.8	**7.1**	6.5	8.5
Bronco Valley	2012	79	**16.6**	8.7	28.7	**15**	13.5	18

Home range

Between September 2010 and June 2013, 60 cats were captured. Three cats were caught in wire cage traps (265 trap nights), 19 in leg-hold traps (940 trap nights) and 38 by spotlighting or netting with the help of trained cat-detection-dogs (221 hours). Of the 60 cats, we placed GPS collars on 37, and obtained at least one month of GPS data from 32 of these. There was a strong male bias in this sample of cats. Males comprised 78 % of all captured cats (47 of 60) and cats from which GPS data were obtained (25 of 32). We generated kernel density estimates and derived 95 % isopleths for the 32 cats with at least one month's GPS data. There were 14 shifts in home range during data collection; 11 of these were classed as long-distance and temporary travels and not considered in this paper, while the remaining three shifts were used in analysis (that is, separate estimations were made of home ranges before and after the shift for these three cats). In total, we obtained 35 estimates of home range for 32 cats.

On average, home ranges were 760 ha (range 120 ha to 2106 ha, n = 35). Male home ranges (855 ha, 95 % CI ± 156, n=25) were on average twice the area of female home ranges (397 ha, 95 % CI ± 275, n=7). The most parsimonious model to describe home range size included sex, weight, and percent of alluvial vegetation (AICc delta of 0, and 2.04 for next strongest model). Male home ranges were, on average, larger than females' ($t = 2.5$, $P = 0.02$); home

range area increased with cat weight (t = 2.1, P = 0.04); and home ranges were significantly smaller for cats with more riparian vegetation within their home range (t = -3.2, P = 0.003). There was approximately a 10 % reduction in home range size for each 10 % increase in alluvial vegetation (see Figure 4).

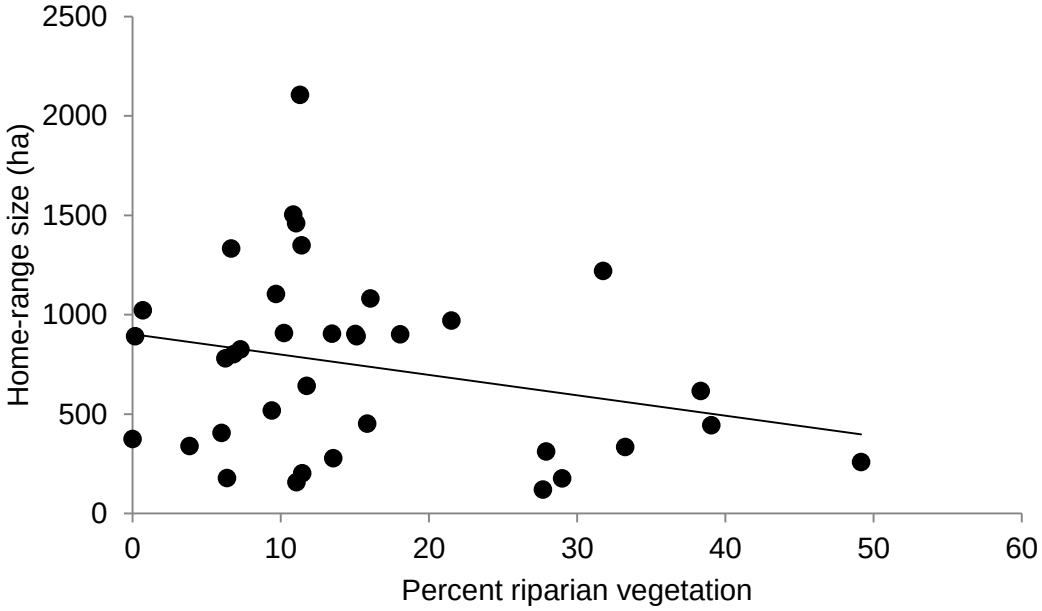

Figure 4. Estimated male feral cat home range size against the percent of riparian habitats within their home range.

There were 24 instances of cats with overlapping home ranges in the dataset. Of these, 14 were male-male, and 10 were male-female. We recorded no instances of female-female overlap. Adult male cats displayed discrete home ranges with little overlap, 5.6 ± 2.3 % CI (see examples in Figure 5). There was extensive male-female overlap (range 0.1 to 100 %), with overlap values relatively uniformly distributed across this range.

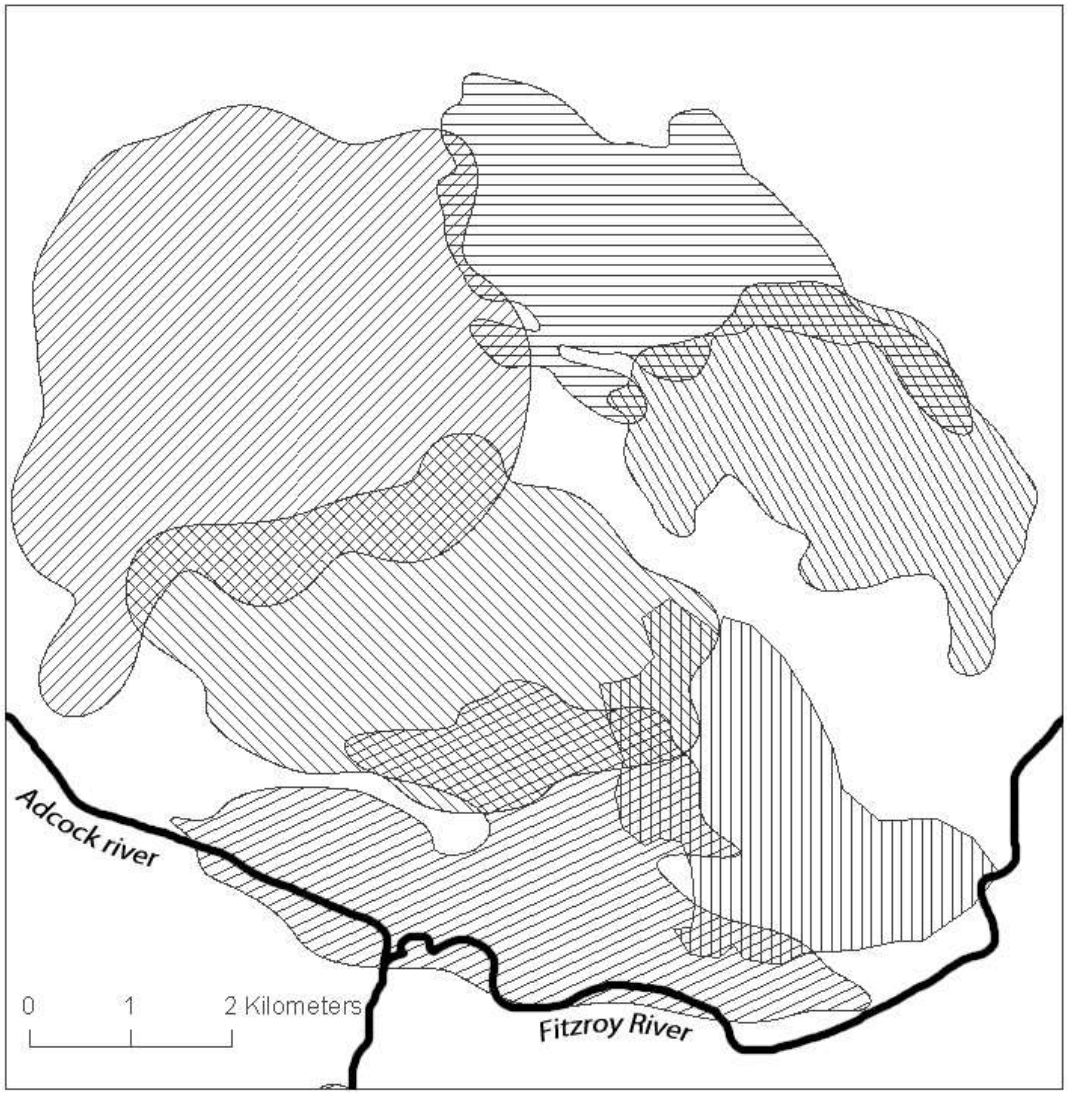

Figure 5. Example of home range overlap in male feral cats, with each cross-hatched shape the boundary of concurrently recorded home range created using kernel density analysis at a 95 % isopleth. There were no other male cats collared in this region.

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Discussion

Feral cats occur at low density in the central Kimberley, with an average of 0.18 cats per km^{-2} from the 13 sessions measured. Even the highest mean density on any transect (0.34 km^{-2}) was lower than the mean densities reported in all other studies outside of the arid zone (0.7 km^{-2} or more; Bengsen *et al.* 2012; Denny and Dickman 2010; Jones and Coman 1982). Most of these other estimates used sighting transects (cats being counted at night from a moving vehicle and detected with a spotlight), which are likely to underestimates densities of cryptic animals like cats. Corresponding with low density, home range sizes of cats in our study region were large compared to those reported in other studies outside the semi-arid zone (e.g. Bengsen *et al.* 2012; Buckmaster 2012; Johnston 2012), suggesting they require large areas to obtain adequate amounts of food. We do not yet know whether many other areas across the northern Australia also have such low densities, however, this is possible as most known activity measures report few cat detections (Ibbett 2010; Kennedy *et al.* 2012). Our study provides a baseline estimate for the central Kimberley, and an indication of likely densities of cats elsewhere in northern Australia.

Our modelling of population density hinged on the ability to identify individual cats. While the vast majority of cat passes were reliably identifiable to an individual (96 %), the remainder could be assigned only on a subjective assessment of body shape. Such cats were present in four of the 13 sessions. Whilst this could not be verified, we compared population estimates of the four sessions affected to estimates from a non-spatial mark-resight model, and found a strong convergence of estimates. This suggests that errors due to misidentifying this small portion of cats would not dramatically skew the overall results. While we were fortunate to study populations in which such a high proportion of cats were identifiable from photographs, this might not be the case in other populations. In such instances, spatial mark-resight analysis would be essential (Chandler and Royle 2013).

A useful aspect of the approach in this study was the ability to incorporate the spatial layout of camera traps into a standardised capture-recapture model. Cats are difficult to attract with lures when at low densities, and often show strong variations in lure preferences between areas and times (Edwards *et al.* 1997; Kilshaw *et al.* 2014; Short *et al.* 2003). This method

essentially allowed us to place the cameras where the cats would naturally occur along each of transect, as opposed to drawing the cats towards the cameras with a lure.

Our use of almost-linear transects had both positive and negative effects on analysis. Deploying cameras for each session was logistically simple, so multiple arrays could be set with relatively few detectors. Alternatively, a grid pattern would have meant far fewer arrays could have been operated per year. However, each individual transect had quite large errors, and 95 % confidence limits were often double or half the mean. These transects would have had lower errors had we used grids, because for cats detected at the ends of transects there was high uncertainty in the estimation of location of the home range centre. Nonetheless, there was strong agreement in densities measured on different transects and in different times. Therefore, this method appeared robust in its estimation of broad-scale cat densities, but provided less precise estimates at the transect scale. Future use of this method should adapt a grid-like form wherever possible.

We did not find any significant spatial or temporal variations in density. However, the large confidence intervals at each transect would mean only large changes would have been detected. To assess whether there could have been smaller changes, we compared home range size in relation to landscape features, because home range size is inversely related to density, especially in territorial species (Liberg *et al.* 2000). Home range size was smaller for cats with greater amounts of riparian vegetation. Home range size in terrestrial mammals is typically related to resource availability, so riparian areas likely provide a higher concentration of food (Gittleman 1985). Small mammal abundance is typically higher in such habitats in the study area (Legge *et al.* 2011a). However, the effect on home range size was not large. It is likely that density would also be greater in areas of higher riparian cover, but the effect size was too small to detect with our camera-trap study.

Contrary to expectations, we did not detect either cat density or home range size to change with grazing from introduced herbivores, despite substantial variation in small-mammal abundance between the stocked and destocked zone (Legge *et al.* 2011a). We suspect that there was little correlation between grazing regime and cat abundance as small mammals would be protected from predation by grass cover in ungrazed areas, so cats were less able to exploit these populations. Whilst fires would have temporality removed such cover, the

frequency and extent of such fires was similar between the stocked and destocked zone (Legge *et al.* 2011b). Overall, although prey abundance was higher in ungrazed areas, prey accessibility was not, so perhaps the availability of prey to cats was no higher than in grazed areas.

Despite their low abundance, cats are contributing to the collapse of small mammal populations now underway across northern Australia (Fisher *et al.* 2013; Frank *et al.* 2014; Woinarski *et al.* 2011b). Evidently, even low-density populations of cats can have large impacts. For example, populations of native Australian rats *Rattus villosisimus* reintroduced to Wongalara, in the Northern Territory, were hunted to extinction soon after release by only one or two individual cats (Frank *et al.* 2014). Other instances of a seemingly scarce population of cats causing declines of native animals have been reported (Gibson *et al.* 1994; Moseby *et al.* 2012a; Priddel and Wheeler 2004). Unlike most other threatening species, the impacts of feral cats need not be driven primarily by their abundance, but by other aspects of their ecology. It may be in part the ability of cats to selectively hunt in habitats where prey are vulnerable (Chapter 3), indulge in surplus killing (Peck *et al.* 2008, Chapter 5), and specialise on particular prey (Fitzgerald and Turner 2000).

It will be very difficult to accomplish significant reductions of populations of feral cats by direct control (e.g. hunting), considering the low densities reported here. For direct control in an open population to be successful, off-take needs to be greater than recruitment (Hone 1999). McCarthy *et al.* (2013) simulated a population of 200 cats, and found at least 57 % would need to be removed annually to sustain a 25 % decrease in population size. If we aimed to reduce population density of cats in the Mornington Wildlife Sanctuary (3200 km^2) by 25 % by removing 57 % annually, we would need to capture approximately 308 of our estimate of 521 individual cats each year. Considering the capture rate densities reported here of 1 cat per six hours of spotlighting, we would need to spotlight for almost 1840 hours, or five hours every night of the year. This does not even consider declining success as density decreases, learned aversion by cats, and incomplete coverage of the region. While poison baiting can provide landscape scale reductions of such magnitudes in some circumstances (Johnston *et al.* 2011; Moseby *et al.* 2009), this method is unlikely to be applicable in northern Australia due to risks to non-target predators such as dingoes and northern quolls *Dasyurus hallucatus*.

Future improvements in cat control methods could make off-take greater than recruitment, especially if automated devices could ensure that every cat passively detected could be either killed or sterilized (Read *et al.* 2014). Considering the detection rates here of 0.31 over three nights at home range centre (g0 in Table 1), and that they remain over 0.01 for over a kilometre from this centre (based on sigma values in Table 1), most cats would be killed by such a device if left within its home range for around three months. However, such technology is still not yet available.

Due to the virtual impossibility of landscape scale cat control using existing methods when densities are low, other methods of reducing their impact on native wildlife will have to be considered. Maintaining dingo populations may provide top-down control (Kennedy *et al.* 2012; Moseby *et al.* 2012b). Cat exclusion could be considered at small scales around critical habitats, either using fences (Moseby and Read 2006) or guardian dogs (van Bommel and Johnson 2012). Otherwise, land management practices that reduce the impacts of cats, as opposed to reducing their densities, should be considered over large scales.

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CHAPTER 3

Landscape management of fire and grazing regimes alters the fine-scale habitat selection by feral cats

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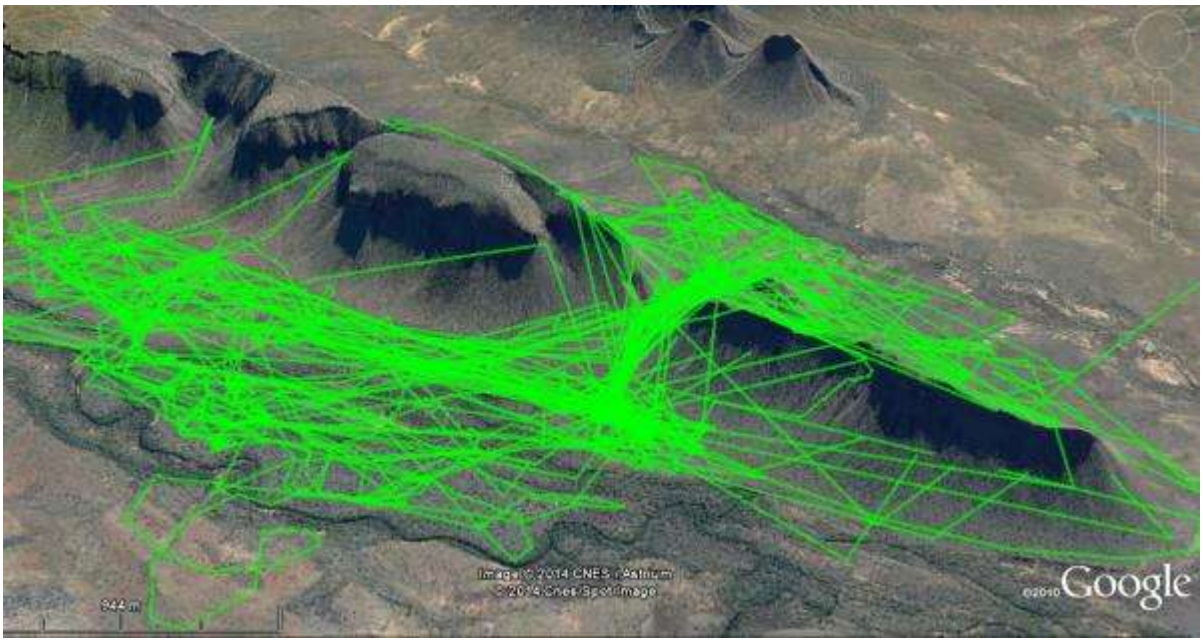

GPS movements of a feral cat around Mt Hamilton, WA

Abstract

Intensification of fires and grazing by large herbivores has caused population declines in small vertebrates in many ecosystems worldwide. Impacts are rarely direct, and usually appear driven via indirect pathways, such as changes to predator-prey dynamics. Fire events and grazing may improve habitat and/or hunting success for the predators of small mammals, however, such impacts have not been documented.

To test for such an interaction, we investigated fine-scale habitat selection by feral cats in relation to fire, grazing and small-mammal abundance. Our study was conducted in north-western Australia, where small mammal populations are sensitive to changes in fire and grazing management.

We deployed GPS collars on 32 cats in landscapes with contrasting fire and grazing treatments. Fine-scale habitat selection was determined using discrete choice modelling of cat movements.

We found that cats selected areas with open grass cover, including heavily grazed areas. They strongly selected for areas recently burnt by intense fires, but only in habitats that typically support high abundance of small mammals.

Intense fires and grazing by introduced herbivores created conditions that are favoured by cats, probably because their hunting success is improved. This mechanism could explain why impacts of feral cats on small mammals in northern Australia might have increased. Our results suggest how the impact of feral cats could be reduced in most ecosystems by maximising grass cover, minimising the incidence of intense fires, and reducing grazing by large herbivores.

Introduction

Predator-prey relationships are strongly influenced by the structure and quality of habitat, principally its vegetation (Didham *et al.* 2007; Griffiths 1975; Lima and Dill 1990). Variability in vegetation structure may be used by predators to increase hunting success. For example, lions use dense vegetation to hide their approach from prey (Hopcraft *et al.* 2005). Also, it may be used by prey to help them evade predators, such as elk using woodlands as a refuge from wolves (Hebblewhite *et al.* 2005). Changes in habitat structure may therefore shift the relationships between predators and prey (Dickson and Beier 2002; Koenen *et al.* 1996). Such changes can determine the extent to which some prey are threatened with extinction by heavy predation (Didham *et al.* 2007; Gilliam and Fraser 1987).

One of most pervasive impacts on vegetation structure arises from changes to fire and grazing regimes. While drivers of such changes vary immensely, the impacts on fauna communities display some general trends. For example, small mammal populations are especially sensitive, with the vast majority of studies detecting declines in populations in response to either intense fire events or intense grazing (Banks *et al.* 2011; Horn *et al.* 2012; Jones 2000; Tabeni and Ojeda 2003; Yarnell *et al.* 2007), unless they occur in ecosystems with few predators (Conner *et al.* 2011; Southgate *et al.* 1996). The underlying mechanisms of these declines remain elusive, but are likely to be indirect, rather than through direct effects such as being burnt by the fires or trampled by cattle (Driscoll *et al.* 2010). Instead, such disturbances may improve habitat for predators in ways that increases their impacts on prey (Fisher *et al.* 2013; Sutherland and Dickman 1999; Yarnell *et al.* 2007), although no field data are available to confirm this.

Many small mammal species are declining in the savannas of northern Australia, and several may soon be threatened with extinction (Fisher *et al.* 2013; Woinarski *et al.* 2011a). Declines have been greatest in areas subject to intense fires (Firth *et al.* 2010; Pardon *et al.* 2003) and recent experimental evidence also supports an association of grazing by introduced herbivores (cattle, horses, donkeys, buffalo) with the magnitude of small-mammal decline (Legge *et al.* 2011). Both fire and grazing regimes in northern Australia have intensified substantially over recent decades in ways that could contribute to the contemporary native

mammal decline. These changes to fire and grazing have generally made grass communities less complex and more open (Liedloff *et al.* 2001).

Predation by feral cats *Felis catus* may also be contributing to the declines. This is suggested by three lines of evidence. First, the declining species fall within the preferred prey-size range of cats (Dickman 1996; Fisher *et al.* 2013). Second, mammal populations in complex rocky habitats have been less affected than those in more productive woodlands and savanna, suggesting a predation effect (Oakwood 2000; Radford *et al.* 2014). Finally, populations of declining mammal species are more stable in the absence of cats, on island or in large enclosures (Frank *et al.* 2014; Woinarski *et al.* 2011b). However, there is a temporal mismatch between the arrival of cats in northern Australia (up to 170 ya in some places; Abbott 2002) and mammal declines observed in the last 20 years (Woinarski *et al.* 2011a).

The apparent mismatch in timing of the early arrival of cats and recent mammal declines could be explained by the hypothesis that cat predation has its largest impact when it interacts with fire and grazing regimes established in the more recent past. Reduction of structural complexity of vegetation and increased openness due to fire and grazing might increase the exposure of small mammals to predators, making prey easier to detect and capture (Conner *et al.* 2011). Small mammals are cats' preferred prey (Dickman 1996; Kutt 2012). If cats preferentially use the open and relatively simple habitats created by fire and grazing, the result could be a higher predation impacts on small mammals. This has been suggested as a possible mechanism for these declines (Woinarski *et al.* 2011a; Ziembicki *et al.* 2013), however, until now there has been no evidence.

If cats do favour the conditions created by fire and grazing, this should be revealed by the patterns of movement of individual cats in heterogeneous landscapes with variable effects of fire and grazing. We tested this hypothesis using intensive GPS tracking of a large sample of individual cats; both within and outside of a large 40 300 hectare area that has been destocked of all introduced herbivores (cattle, horses, donkeys) (Legge *et al.* 2011), and spanning contrasting fire patterns (mild control fires or intensive wildfires). A dynamic habitat map was created, so that fire and vegetation attributes at any location or point in time could be determined. This was used to generate a parsimonious model of fine-scale habitat selection by cats. We predicted that feral cats would select for open grass cover to improve hunting

success. If so, we hypothesise that cats would increase their use of habitats that have been recently burnt or intensely grazed, and that this relationship would be stronger in areas of high small-mammal abundance.

Materials and methods

Study area

Our study area encompassed three large properties in the central Kimberley of north-western Australia (17°01'S, 126°01'E, see Figure 1). One property is managed for commercial cattle production (Glenroy, 1455 km^2) and two are ex-pastoral leases managed for conservation by the Australian Wildlife Conservatory (Mornington and Marion Downs Sanctuaries, 3225 km^2 and 2676 km^2 respectively). Habitats are mostly savanna woodlands with a perennial grass layer, dissected by riparian vegetation along the edges of creeks. The region has a tropical monsoon climate with three broad seasons: the wet (December – March), early dry (April – July) and late dry (August – November). Fire is managed on all three properties to promote biodiversity values. This fire management aims to reduce the incidence of extensive, high intensity uncontrolled fires in the late dry season using strategic prescribed burning in the early dry season, when fires tend to be small and of low intensity because of weather and condition of the grass layer. In addition, when uncontrolled late dry season fires occur, they are suppressed where possible. All large introduced herbivores (cattle, horses, donkeys) have been removed from a 40,300 ha fenced section of Mornington since 2005 (Legge *et al.* 2011), hereafter referred to as the 'destocked' zone. Dingos are not persecuted in the study area, and occurred at a density of ~0.2 individuals per km^2 (Legge *et al.* 2014).

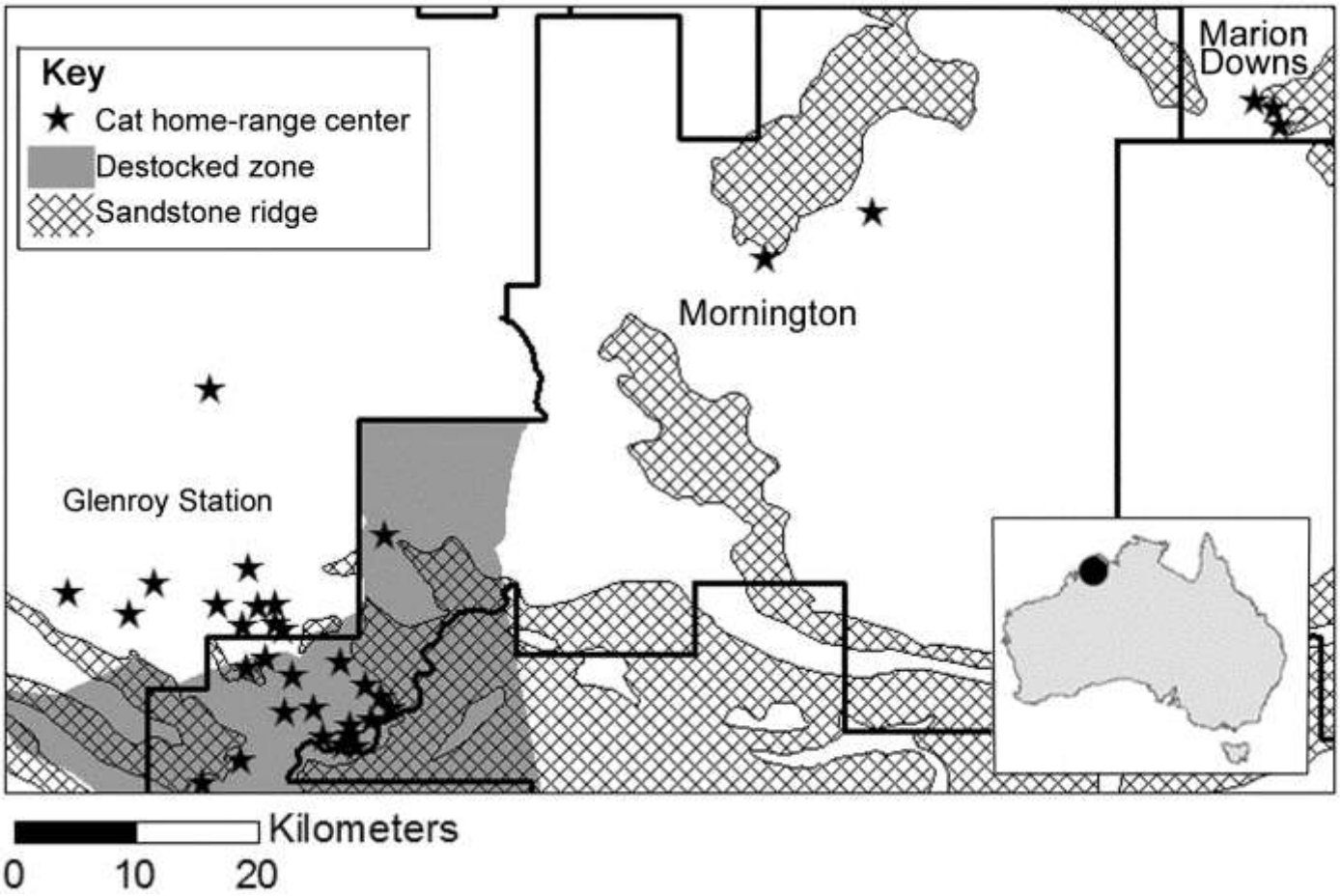

Figure 1. Map of study area in the central Kimberley of north-west Australia (see inset), including home-range centroids of feral cats used in this study.

Cat capture and tracking

Feral cats were captured between September 2010 and June 2013, using either large wire cage traps, leg-hold traps (soft-jaw, size #1.5) or by spotlighting and netting with the assistance of dogs trained to locate and bail cats up trees. If a cat was either bailed up a tree or required examination of possible injury, it was sedated with Zolotil at a rate of 0.5 cc / kg via intramuscular injection. Cats were fitted with GPS collars (Telemetry Solutions Quantum 4000). Cats weighing between 2 and 3.3 kg were fitted with a 70 g collar, and those weighing more than 3.3 kg were fitted with a 100 g collar (< 3 % of body-weight). Sedated cats were released after full muscle control was regained (4 – 6 hours later), non-sedated cats were released as soon as possible (2 – 5 minutes later). When it was necessary to replace GPS collars, the cats were recaptured using the dogs.

GPS collars were deployed on equal numbers of cats in the stocked and destocked zone, and between burnt and unburnt areas. Within burnt areas, the cats were split evenly between areas with low and high intensity fires. The GPS units were programmed to record fixes every 15 minutes for two-day bouts, starting and finishing at 12 pm. These bouts were separated by intervals of one, two or fourteen days. All bouts were timed to commence at least 24 hrs after the cat was handled. Units were programmed to search for a satellite for 60 seconds, and to remain on for at least 5 seconds to refine the fix if there was memory from the last fix, or 15 seconds if not.

Habitat variables

Across the study area, we developed habitat maps relating to fire and grazing, along with any other variable likely to influence cat habitat selection or movement. Where necessary, the maps were updated to make them temporally dynamic, so that attributes at any given time and location could be determined. Most descriptors of habitat related to the ground layer, rather than the tree layer. Nine distinct grass communities common in the region (see Table 1) were mapped by examining colour disjunctions on aerial photos while altering light levels in Photoshop Elements v. 8, tracing the boundaries of discrete polygons onto the aerial photos, then geo-rectifying these boundaries in ArcGIS v.10. For example, spinifex *Triodia* spp. grasslands are uniquely green in dry-season aerial photos, while communities dominated

Table 1. Vegetation communities mapped in the study region. Vegetation classes are ranked by their preference for grazing by domestic stock, with 9 the most impacted and 1 the least (Grazing rank). Small mammal abundance is number of small mammals captured per 60 trap nights, in the stocked and destocked zone, from 2011 to 2013.

		Grazing	Small mammal abundance					
		rank	Stocked			Destocked		
Grass community	Dominant grasses		2011	2012	2013	2011	2012	2013
Riparian forest[A]	*Chrysopogon fallax*	1	0.2	0.3	0.8	1.2	3.4	9.4
	Mnesithea rottboellioides							
	Various introduced grasses							
Alluvial grasslands[A]	*Crysopogon fallax*	2	0.2	0.3	0.8	1.2	3.4	9.4
	Dichanthium fecundum							
Bluegrass plains	*Aristida* spp.	3	1	1.3	4.6	0.3	2.6	2.9
	Dichanthium fecundum							
Canegrass[A]	*Mnesithea rottboellioides*	4	0.2	0.3	0.8	1.2	3.4	9.4
Mixed woodlands	*Aristida* spp.	5	0	1.3	0.6	0.2	3.8	6
	Dichanthium fecundum							
	Heteropogon contortus							
Sandseep	*Triodia* spp.	6	1.7	1.2	1.2	1.8	7.4	16.8
Hillside woodlands[B]	*Sehima nervosum*	7	0	0.6	1	0.4	3.2	4
Spinifex woodlands[B]	*Triodia* spp.	8	0	0.6	1	0.4	3.2	4
Bare ground	No or little	9	0	0	0	0.2	0.2	0.5

[A] and [B] denote grass communities where the small mammal abundance was grouped, as sites were typically larger than the mapped distributions of these communities.

by bluegrass *Dichanthium fecundum* are white. The digital map was ground-truthed at 768 plots (described later); the attribution of grass community was correct at 96 % of sites.

Fire extents were initially mapped using monthly Landsat 7 remote-sensing imagery available from the US Geological Survey (2011–2013), and fire boundaries were then refined using aerial photography taken from a helicopter flying approximately 300 m above ground. For each burnt area, we assigned the date of burn and intensity (intense = 100 % tree scorch and no ground cover remaining unburnt, or mild = all other fires). Relative to the date of each GPS fix, fire was considered in multiple binary variables at 30, 60, 90, 180, 360 or 600 days since fire. The Australian Wildlife Conservancy's stock-proof fence (Legge *et al.* 2011) separated the stocked and destocked areas.

A dynamic map was created that estimated grass cover at any given location and time since fire, based on a series of models of response of the grass layer to fire (given grass community, stocking status) created from field data. Vegetation attributes were measured at 768 plots (each 10 m^2) across the study area and duration, spread equally across grass communities (see Table 1) and combinations of mild / intense fire, time since fire, and grazed and destocked areas (total of 96 plots per community). At each plot, we estimated the extent of grass cover at different heights by adapting a line-intercept method. We inserted a 100 cm pole (diameter of 1.5 cm) vertically through the grass to the ground at 50 points in a systematic grid over the plot. The number of grass intercepts was recorded in height intervals of 0 – 10 cm, 11 – 30 cm, and 31 – 100 cm. This was used to derive grass cover, cover of dense tussocks, and relative biomass at each plot (see Appendix 1 in supplementary material for more detail on methods). These variables were modelled against grass community, time since last fire, intensity of fire, and stocking status. Models were then used to derive values for all GPS fixes and random points used in discrete choice models (see Appendix 1).

The influence of grazing on grass biomass was measured as the difference in the average total number of grass intercepts per plot between grass communities in the stocked and destocked sites. We used only unburnt sites for this comparison. These averages were converted into a grazing impact rank. However, these variables would be confounded by correlation as the habitats favourable to cattle would also be favoured by feral cats (e.g. riparian areas), irrespective of impacts of cattle. Therefore, this score or rank was applied to all fixes, grazed or not, and the actual impacts of cattle grazing considered as the difference in this variable's strength between the destocked zone and outside.

Relative small-mammal abundances in different habitats were estimated from the Australian Wildlife Conservancy's annual fauna monitoring data, which is carried out across all three properties (Legge *et al.* 2014). The sample at each site is based on 20 small mammal box traps (Elliott traps) set for three nights (60 trap nights), spread over 1 ha. There were 55 to 64 sites sampled each year totalling 176 site-years between 2011 –13. Small mammals were defined as those weighing between 30 g and 2000 g (based on Dickman 1996; Fisher *et al.* 2013), and were predominantly *Rattus tunneyi* and *Pseudomys nanus* (these species comprised 87 % of captures). For each year, average rates of capture of individual small mammals were calculated for each grass community in the grazed and destocked areas (see Table 1). However, as sites were typically larger than the mapped patterns of these grass communities, results from some communities were combined (see Table 1). In case cats altered their response to a threshold of small mammal abundance, we also included three binary variables of abundance (whether there was more than 1, 2 or 5 small mammal captures per plot) for each habitat.

We measured other spatial and temporal features likely to be important to cats to provide context for their movements. As cats may prefer hunting on edges between open and dense vegetation, we delineated a 25 m buffer either side of any linear boundary where grass cover was < 25 % on one side and > 50 % on the other (these were most often fire edges). Water features were mapped in the field, and each assigned a descriptor for the seasons that they contained water (wet season only, wet and early dry, or year-round). This was used to derive distance to known standing water at any given time throughout the study. Elevation and slope were derived from a digital elevation model of 15 m resolution. We created a variable representing the spatial home-range context for each cat, by making a kernel density estimate (smooth cross-validation) for all moving fixes of each cat, and delineating kernel isopleths at 50 %, 90 %, 95 % and 99 % contours. Temporal variables included time of day (sun time; Torre *et al.* 2007), season (wet, early dry or late dry), number of months since the end of the wet season, and minimum nightly temperature (HOBO temperature data logger, MicroDAQ). Finally, a cat's choice of which habitat to select in successive GPS fixes may be dependent on the type of habitat it was last in. This spatial correlation might arise when an animal selects for certain landscape features and tends to remain within them for some time, rather than making a *de novo* selection at every 15 min interval of their walk. Therefore, we fitted a

binary ‘carry-over’ variable, which described whether the vegetation, grazing and fire values were equal to the previous fix.

Data analysis

All GPS fixes that were likely to be erroneous, biased or to represent a stationary cat were removed from the analysis. Erroneous fixes were those representing implausible ‘spikes’ in movement, presumably caused by GPS error (Bjørneraas *et al.* 2010). We deemed it unlikely that a cat would suddenly change course and speed, then return to the same area it was in 15 minutes ago, so spikes were defined where fixes met all the following criteria: distances from the last fix were > 50 m, difference in distance from the preceding and succeeding fix was < 10 %, and turning angle > 170° (based on Bjørneraas *et al.* 2010; Recio *et al.* 2014). The HDOP values were not used to filter fixes, as a test of six GPS collars found no relationship between HDOP and distance from the GPS fix to the known location. Fixes that were potentially biased by human disruption of the behaviour of the cat were removed, being those within three hours of field VHF tracking (this was occasionally carried out in order to download data remotely from the cat GPS collar). Fast-moving fixes were also removed, as it was likely cats were moving away from something, rather than choosing habitat. For this purpose a filtering speed of greater than 2 km/hr was used, as this was where the histogram of speeds between fixes reached an asymptote (Recio *et al.* 2014), representing a shift in behaviour mode. A test of GPS error within the open savanna found that 95 % of fixes had < 5 m error (from 634 fixes on six different collars), so fixes less than 10 m from the preceding fix were classed as stationary. We considered only moving fixes, as cats may have different habitat requirements for resting versus hunting.

Habitat selection by cats was analysed using discrete choice modelling (Cooper and Millspaugh 1999). The range of ‘available’ habitats was calculated for each fix, and then we compared the option selected by the cat to the available habitats. To find the available habitats, we first constructed probability distributions of a cat’s step-length and turn angle over 15-minute intervals, then used these probability distributions to select five random points to sample the cat’s options (Cooper and Millspaugh 1999). Each GPS fix and associated random points were attributed with the habitat variables of interest using the dynamic vegetation map.

We determined resource selection by cats by creating models with all combinations of variables, including different biologically relevant interaction terms, and comparing them within an information theory framework (Burnham and Anderson 1998). This produced a total of 916 models. For each interaction term a model was included with all combinations, or with only significant combination terms retained. No pairs of variables with Pearson's correlation greater than 0.5 were included in the same model. Models for habitat selection were created using standard case-control logistic regression models, implemented in R (R Development Core Team 2008), using the 'clogit' command from the 'survival' library. Each individual cat was considered as a random effect in the models, using Gaussian frailty (Therneau *et al.* 2003). The most parsimonious models of cat habitat selection were chosen as those with an AIC score within two points of the highest-ranked model (Burnham and Anderson 1998), and only these are presented in the results. The cat's selection is measured as an odds ratio, representing the magnitude of change in the odds of selection for each unit of the predictor variable. Differences in the odds ratio are relative only to the other habitat choices immediately available to a cat.

Results

In total, 60 cats were captured between September 2010 and June 2013. Three cats were caught in wire cage traps (265 trap nights), 19 in leg-hold traps (940 trap nights) and 38 by spotlighting/netting with trained cat-dogs (221 hours). GPS collars were placed on 37 cats, and at least one month of GPS data was obtained from 32 cats, spread equally across stocking and fire management treatments (Table 2). There was a strong male bias in the sample of cats: males comprised 78 % of all captured cats (47/60) and cats from which GPS data were obtained (25/32). Of the GPS-collared cats, four had disappeared and their fates were unknown at the end of the study, nine had died naturally, and the rest were euthanased.

Table 2. The number of cats fitted with GPS collars, in each of the different grazing and fire treatments. Destocked means that all introduced herbivores are excluded.

Management	No fire	Mild fire	Intense fire	**Total**
Stocked	8 (5♂ 3♀)	4 (3♂ 1♀)	4 (3♂ 1♀)	**16**
Destocked	8 (6♂ 2♀)	4 (4♂)	4 (4♂)	**16**
Total	**16**	**8**	**8**	**32**

From the 32 cats that provided useable GPS data, we obtained a total of 133 047 GPS fixes. Cats were moving 56 % of time. Of these moving fixes, 62 % were at night (between sunset and sunrise). Removal of erroneous or biased fixes and those representing high-speed movement left 38 472 choices for habitat between successive 15-minute moving fixes.

From the 916 models generated to describe habitat selection by cats, three were ranked within the candidate model set (the model with the lowest AIC score and two other models within two AIC scores of the top model). The top model carried 41 % of the weight, compared to 24 % and 20 % for the second and third ranked models. Of these, the second and third ranked models were almost identical to the top model, but contained interaction terms that did not decrease the models AIC value. As these terms did not improve the maximum likelihood for these models, only the top model was considered further (Table 3).

The top model included negative selection for grass cover (equivalently, positive selection for open areas) and positive selection for edges (see Table 3). Both variables had a significant interaction with small-mammal density in a binary format (> 2 captures per 100 trap nights), showing that cats selected particularly strongly for open areas in habitats with higher density of small mammals.

Table 3. Statistics of the top ranked model of cat habitat selection, based on GPS data at 15 minute intervals from 32 individuals. The odds ratio is the change in selection likelihood per unit of the variable.

Variable	Odds ratio	robust SE	Z	Pr(>|z|)	
Grass cover with scarce small mammals [a]	-1.26	0.08	-2.88	0.004	**
Grass cover with abundant small mammals [a]	-1.85	0.1	-6.44	0.0001	***
Bare / grass edge with scarce small mammals [a]	1.2	0.07	2.81	0.005	**
Bare / grass edge with abundant small mammals [a]	1.41	0.06	6.26	< 0.0001	***
Fire scar < 360 days	-1.32	0.07	-4.09	< 0.0001	***
Intense fire scar < 360 days old	1.54	0.13	3.29	0.001	**
Intense fire scar < 90 days old	-2.11	0.13	-5.67	< 0.0001	***
Small mammal abundance (square-root)	3.52	0.21	6.03	< 0.0001	***
Small mammal abundance, intense fire scar < 360 days	-4.93	0.66	-2.4	0.0163	*
Small mammal abundance, intense fire scar < 90 days	10.71	0.79	2.99	0.0028	**
Grass communities ranked on grazing impacts, in:					
- stocked areas during day	5.96	0.14	12.56	< 0.0001	***
- destocked areas during day	3.52	0.25	5.07	< 0.0001	***
- stocked areas over night	2.64	0.17	5.65	< 0.0001	***
- destocked areas over night	2.44	0.16	5.67	< 0.0001	***
Water proximity (km) by months into dry season	1.56	0.06	-7.77	< 0.0001	***
- as above, by minimum nightly temperature (10°C)	1.13	0.03	3.94	< 0.0001	***
Elevation (100 m)	-1.93	0.28	-2.32	0.0202	*
Home range isopleth [b], adult female	3.53	0.05	27.17	< 0.0001	***
Home range isopleth [b], adult male	2.28	0.1	-8.41	< 0.0001	***
Home range isopleth [b], sub-adult	1.06	0.49	-0.12	0.9077	
Same habitat as last fix, if within 95 % isopleth	2.06	0.02	41.4	< 0.0001	***

a. Scarce and abundant small mammals are defined as less than or greater than two individuals captured per 60 trap nights at Australian Wildlife Conservancy monitoring sites

b. Home range isopleth derived at 50 , 90, 95 and 99 % contours from kernel density estimator

Fire was represented in the top model with fire scars up to 360 days old, fire scars < 90 days old, whether the fire was intense, small-mammal abundance, and interaction terms between these variables. Once the odds ratios of these variables were combined, cats showed strong positive selection for areas within 90 days after an intense fire and where density of small-mammal prey was high (Figure 2). However, in all other circumstances selection for areas burnt by intense or mild fires was negative.

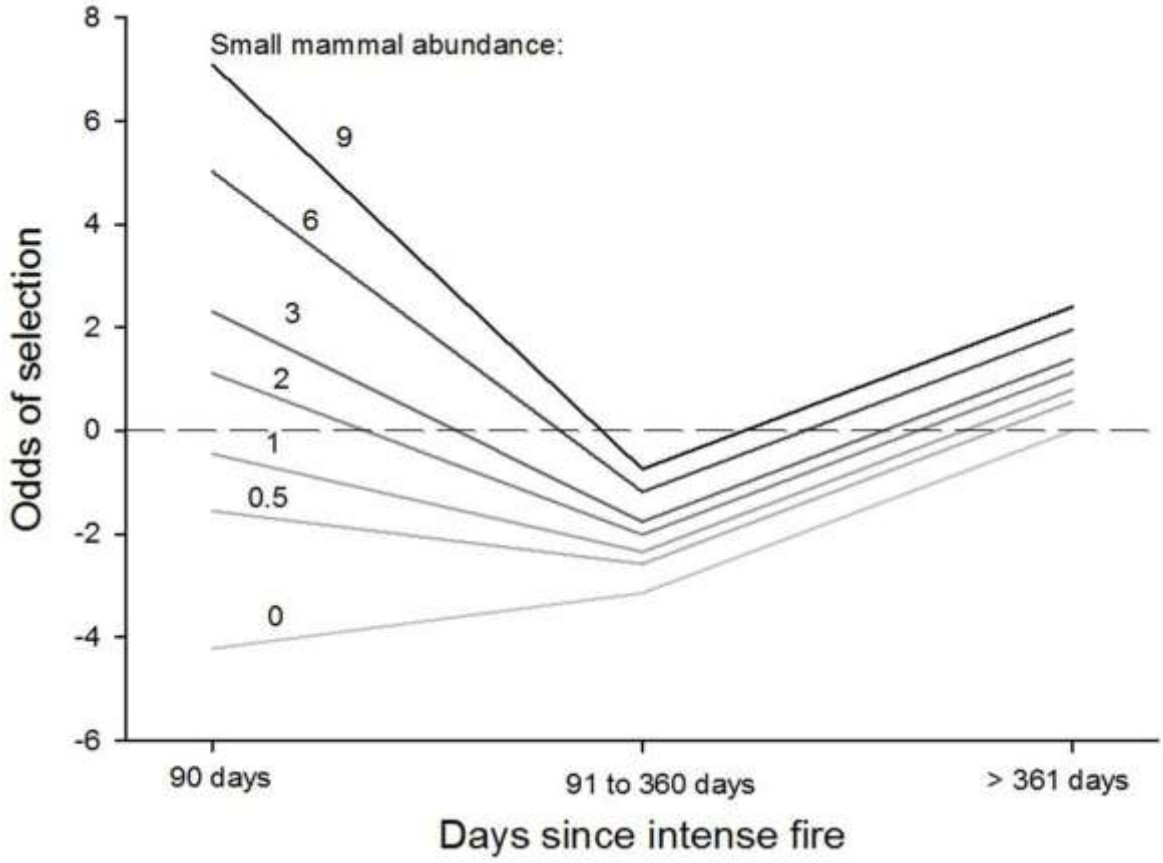

Figure 2. Addition to the odds of selection ratios over long unburnt habitat for different days since intense fires, at different average small mammal abundances based on capture rates per 160 trap nights (ranging from 0 to 9, lighter to darker respectively). All other variables in the model are assumed to be constant (see table 3)

Vegetation types with greater susceptibility to grazing impacts (e.g. riparian areas, Table 1) were strongly selected for in both the grazed and destocked zones. However, this relationship was significantly stronger in the stocked zone than in the destocked zone, especially during the day (see Figure 3).

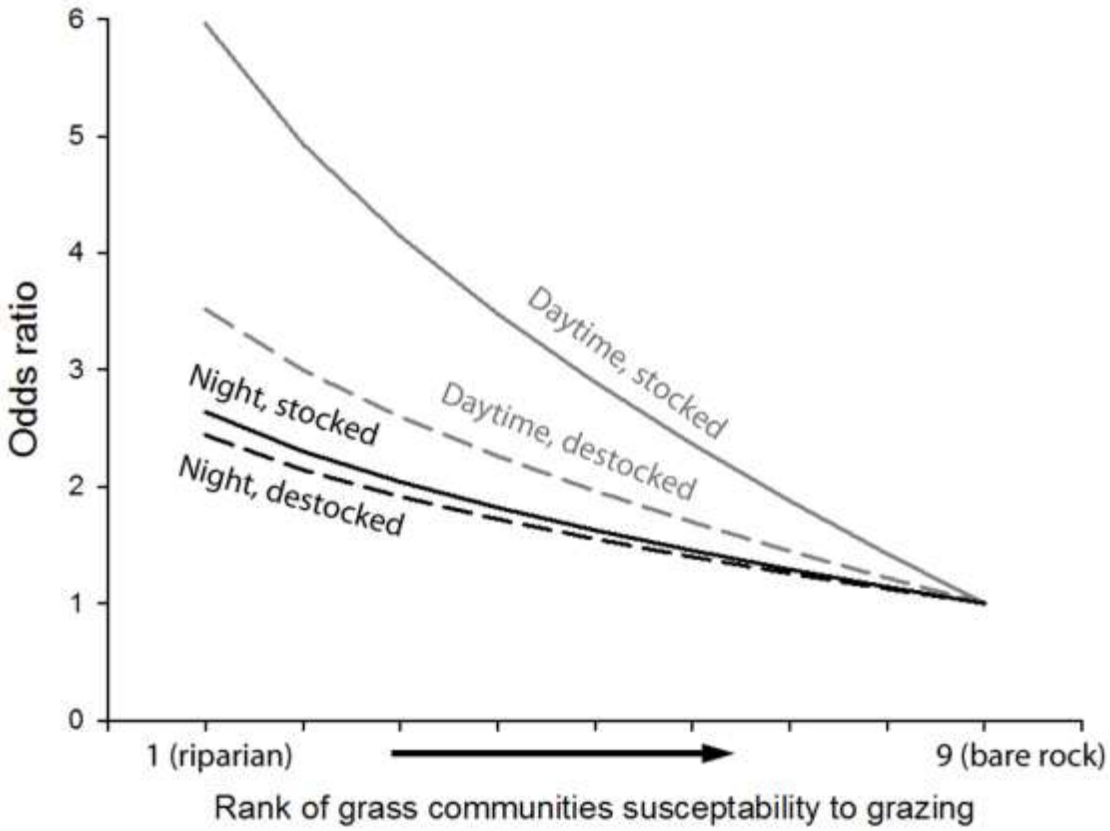

Figure 3. Odds ratios for selection of cats at night (black) and day (grey) in stocked (solid) and destocked (dashed) areas against grass communities ranked by grazing susceptibility. All other variables in model assumed to be constant (see Table 3)

Several other variables influenced selection by cats. Cats chose to move towards water. The odds ratio of moving towards water became progressively stronger throughout the dry season (by 0.56 every month into the dry season) and on days with higher minimum temperature (by 0.13 for each 10° C increase). Cats selected against changes in elevation, with odds declining by 0.93 every 100 m. Cats tended to move into higher-use areas within their home range (determined by kernel density estimates), with an interaction with age and sex. Adult females demonstrated the strongest fidelity to home-range isopleths, while for sub-adults of either sex this was not significant ($P = 0.9$). Cats were twice as likely to select for the same habitats as the previous fix ($P < 0.001$), assuming the fix was inside a cats' home range (95 % isopleth).

Discussion

Our study provides a detailed analysis of the preferences that underlie movement decisions by feral cats in a tropical savanna environment in northern Australia. We show that modifications of habitat produced by grazing and by certain types of fire have strong effects on cat movement behaviour, with the general result that fire and grazing can create habitat conditions which are strongly favoured by cats. When faced with choices about where to move, cats consistently selected sites with a more open grass layer, which had recently been subject to intense fires, and which were heavily grazed. Further, cats' habitat selection in relation to fire was strongly affected by whether the habitats in question supported high densities of small mammals: sites in mammal-rich habitats that had recently been burnt at high intensity were especially strongly favoured.

This interaction between cat movements, fire and grazing regimes may help explain the recent declines in small mammals in northern Australia. The idea that predation by cats might be driving these declines has been doubted because of the mismatch in timing of the introduction of cats and small mammal declines, together with the fact that we have no evidence that small-mammal declines have coincided with increased populations of cats (Woinarski *et al.* 2011a). As our results demonstrate, impacts of cats could have become more severe with the changes in fire and grazing regimes that began around the 1960s, even if cat density remained constant.

Selection by cats for areas with an open grass layer is a consistent finding from other studies on habitat selection by small felids (Moseby *et al.* 2009; Rajaratnam *et al.* 2007), except in situations where moving into open areas leaves them exposed to larger predators (Genovesi *et al.* 1995) or where prey density is low (Hall *et al.* 2009). Our cats' selection for open areas is almost certainly an expression of hunting preferences, as their selection became stronger in areas with higher small-mammal abundances. Although grass cover in itself had a large effect size (odds ratio maximum of 1.8), the effects of grazing and fire patterns on cat movements were much stronger.

Selection for fire scars was strongly dependent on fire intensity and time since fire. In general, cats avoided fire scars up to 360 days after fire. The exception was for recent scars of

intense fires with high densities of small mammals, which created the greatest increase in the odds ratio of any variable in this study. Fire opens up the grass layer, leaving prey more exposed and accessible to predators (Conner *et al.* 2011). Intense fires would create pulses where prey would be easy for cats to catch, provided local abundance of prey was high. Cats did not select for recent mild fire scars, even in habitats with high small-mammal abundance. Mild fires typically leave pockets of unburnt vegetation (Russell-Smith *et al.* 2002), which provide protection for prey (Banks *et al.* 2011). Also, mild fires are often stopped by riparian and alluvial areas (Russell-Smith *et al.* 2003), and such areas act as refugia for small mammals post-fire (Banks *et al.* 2011). Our results suggest that cats are not able to capitalise on vulnerable small mammals after mild fires, but can after intense fires. This can explain why declines of some threatened native mammals have been so dramatic under regimes of consecutive high intensity fires (Firth *et al.* 2010; Pardon *et al.* 2003).

Grazing by introduced herbivores also affected habitat choice by cats. Certain vegetation types (with more palatable grasses) were more preferred by introduced herbivores than others, typically riparian areas and bluegrass plains (Tomkins and O'Reagain 2007). Cats selected for such habitats even when they had been destocked, but grazing intensified this preference. Cats may have a stronger selection for these areas in the grazed zone as lower prey densities (Legge *et al.* 2011) require them to hunt in areas of relatively higher mammal density in order to obtain enough food. Daytime movements of cats were especially affected by grazing, suggesting that grazing creates favourable conditions for hunting of diurnal prey, such as birds (Brown 1982).

Adult cat movements at small-scale 15 minute segments were dictated by their overall home range. Females had a stronger home-range fidelity than males, probably due to the importance of staying near dens that are used for rearing young (Krofel *et al.* 2013). Sub-adults displayed no such home range fidelity as they were probably in the process of creating and defining their home-ranges.

A top-order predator, the dingo *Canis familiaris dingo*, would also have influenced the movements of cats. Over the area and duration of the study, the dingo populations was abundant (0.2 individuals per km^2) and stable (Legge *et al.* 2014), and dingoes would have been a constant threat to cats (Moseby *et al.* 2012). A concurrent study in the same area that

compared GPS movements of cats and dingoes found that although high use areas of dingoes and cats overlapped, cats were constantly avoiding the locations of individual dingoes (Brook 2013). This suggests avoidance of dingoes would have affected the timing of behavioural decisions of cats (Brook *et al.* 2012), but not necessarily by excluding them from certain areas (Wang and Fisher 2012). Considering dingoes potential role in tropic regulation (Radford *et al.* 2014), further research into the relationship between dingoes, cats, and fire and grazing is warranted.

Conclusions

We demonstrate increased predator activity after intense fires and with grazing by large herbivores, which is likely to increase predation rates on small mammals. Small mammals are the preferred prey of cats, and form a substantial part of the diet of cats in the study region (55 % of prey volume, from 33 stomach contents; unpublished data). Furthermore, the preference of cats for open and intensely burned areas was depended on small-mammal abundance, and was reduced for habitats in which abundance of small mammals was low. These patterns of habitat selection by cats correspond with patterns of small mammal populations in mainland northern Australia, outside complex rocky outcrops, where small mammals decline with intensifying fire and/or grazing regimes (Andersen *et al.* 2005; Firth *et al.* 2010; Kutt and Woinarski 2007; Legge *et al.* 2011; Legge *et al.* 2008; Pardon *et al.* 2003; Woinarski *et al.* 2010). Our work supports the hypothesis that the declines in small mammals across northern Australia are driven by cat predation facilitated by simplification of ground layer structure. However, this evidence is not direct, and other possible mechanisms including trophic alterations (Radford *et al.* 2014) and disease (Woinarski *et al.* 2011a) may still have a role. Further research needs to measure whether mortality of prey is greater in more open areas. Regardless, the magnitude of the impacts of cats globally (Loss *et al.* 2012) suggests that our findings provide a general mechanism for prey decline in ecosystems with grass-dominated understoreys.

The results presented here suggest that manipulation of habitat through careful management of fire and grazing could be used to reduce impacts of cats over large landscapes. Reducing the frequency of intense fires and removing introduced herbivores is likely to be beneficial for small mammals, especially if this management is focussed on naturally mammal-rich

habitats, and results in increased ground cover. Vegetation structure is pivotal in creating ideal landscapes for predators to hunt, and/or refuges for prey to hide.

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CHAPTER 4

Long-distance hunting expeditions to intense fire scars by feral cats

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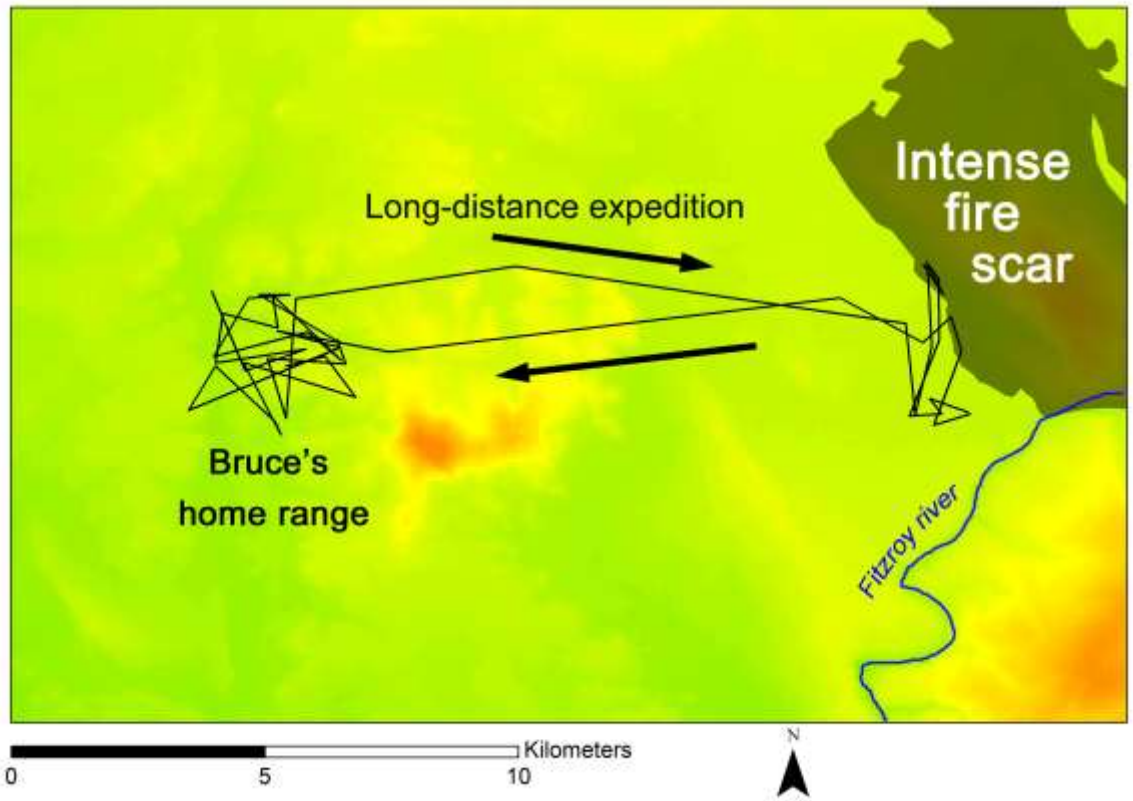
Target journal: *Nature Communications*



GPS data presenting the long distance expedition by the feral cat named Bruce to an intense fire scar 12.5 km away

Abstract

Feral cats are normally territorial in Australia's tropical savannahs, and hunt intensively with home-ranges only two to three kilometres across. Here we report that they sometimes also undertake expeditions of up to 12.5 km from their home ranges to hunt for short periods over recently burned areas. Cats are especially likely to travel to areas burned at high intensity, evidently in response to vulnerability of prey soon after such fires. The movements of journeying cats are highly directed to specific destinations, suggesting advanced spatial comprehension well beyond our current understanding. We argue that the effect of this behaviour is to increase the aggregate impact of cats on vulnerable prey. This has profound implications for conservation, considering the ubiquity of feral cats and global trends of intensified fire regimes.

Introduction

Mammalian predators typically show high site fidelity, and many occupy territories where members of the same species are excluded, either by aggression or mutual avoidance (MacDonald 1983; Wolff and Peterson 1998). Territoriality by predators is an important factor that allows stable coexistence of predators and prey (Wolff 1997). Fidelity to their territories means that predators cannot rapidly change locations to track short-term shifts in distribution of prey (Sih 2005), and this can limit their total impact on prey populations. African lions, for example, occupy stable territories year-round, even in situations where their most abundant prey undergo seasonal migrations and so become inaccessible for part of the year (Hilborn and Sinclair 1979). Territoriality also dampens growth of predator populations, contributing to the lagged response of predator to prey population growth and allowing fluctuating prey populations time to recover from low density in systems with linked predator and prey population dynamics (Korpimäki *et al.* 2004; Krebs *et al.* 2001; Mills and Knowlton 1991; Wolff 1997). In the absence of site fidelity by predators, therefore, predation rates averaged across space and over time can be higher (e.g. Norrdahl and Korpimäki 1996).

Long-distance movement by terrestrial mammalian predators is energetically expensive and physiologically stressful (Hofer and East 1993b; Young and Monfort 2009), and exposes journeying animals to the risk of aggressive encounters with conspecifics (Hofer and East 1993a). Most documented long-distance movements of such predators involve juvenile dispersal (Greenwood 1980; Samelius *et al.* 2012), individuals experiencing dire food shortages (Knick 1990; Packer *et al.* 1990), or dominant males embarking on searches for mates. The rare instances where mammalian predators have been observed making brief extra-territorial movements in search of prey have been to sources of super-abundant food at a fixed location, such as foxes travelling to townships (Tsukada 1997).

Populations of most species of small mammals are currently collapsing in Australia's northern savannahs (Woinarski *et al.* 2011a). There is evidence that intensified fire regimes and predation by feral cats are at least partly responsible for these declines (Fisher *et al.* 2013; Frank *et al.* 2014; Woinarski *et al.* 2011b). But this seems surprising, because cats in the savannahs of northern Australia occur at very low density (mean 0.17 cats.km^{-2}, s.e.m 0.08, in our study area). Also they typically show strong site fidelity and occupy exclusive

territories (Chapter 2), meaning that individual cats are widely spaced. We lack a mechanistic understanding of how sparse populations of this small predator could be having such large impacts on prey.

We show here that cats make predictable long-distance expeditions to hunt intensively at recent high intensity fires far outside their home ranges, and then repatriate to the original home range. These journeys ranged up to 30 km, almost ten times the typical home-range diameter. We analyse the factors that influence cats' decisions to travel, durations of residence at the destination, and finally, the movement rules followed by journeying cats. We argue that the behavioural capacity of feral cats to undertake long-distance excursions to exploit transient hunting opportunities results in significantly higher total predator pressure on prey, and explains how low-density cat populations could have large impacts on small-mammal abundance at landscape scales. This will also have profound implications for global trends of intensified fire regimes (Flannigan *et al.* 2013).

Methods

Study area

Our study area was in north-western Australia, at three large properties in the central Kimberley (17 ° S, 126 ° E). Habitats are savannah woodlands with a perennial grass layer, dissected by riparian vegetation along the edges of creeks. Fire is managed on all three properties to promote biodiversity values. This involves reducing the incidence of extensive, intense fires in the late dry season by lighting strategic prescribed fires with incendiaries in the early dry season when fires are small-scale and mild.

GPS tracking of cats

We studied movements of 32 cats that were captured and had GPS telemetry collars attached between 2010 and 2013. Cats were caught using either large wire cage traps, leg-hold traps (soft-jaw, size #1.5) or by spotlighting and netting with the assistance of dogs trained to locate and corner cats. Collars were set to record one fix per day at 20:00 pm WST, with bouts of fifteen minute fixes each of two days duration (Chapter 3). The single fix per day was used for home range and destination area calculations, while the fifteen-minute fixes were used to measure the properties of the transit passage. The majority (73 %) of transit passages were captured in the fifteen-minute fixes.

Characteristics of movements by cats

To investigate expeditions by cats outside their home-range, we created definitions and 'triggers' for switching between three movement states: within home-range movements, transit, and area-restricted movements at destinations. To define the distinction between within home-range movements and transit, for every fix we determined the distance from the cumulative mean home-range centroid, kept a running standard deviation, and deemed any fix greater than two standard deviations away from this range to represent an abrupt move outside a home-range boundary after at least two weeks of GPS fixes. To differentiate transit from an area-restricted search, we used first-passage time (Fauchald and Tveraa 2003). For all fixes within a sequence outside a home-range, we calculated the first passage time for

circles of 100 m increments, the log-variance for each increment, selected the circle size with the greatest log-variance, and used that size circle to determine area-restricted movements outside a home range. In all instances, home-range movements, transit, and area-restricted movements at destinations were unambiguous (see Figure 1 for examples).

Once travels had been defined, we used discrete-choice modelling to identify determinants of the cats' decisions to travel. Every complete month of active GPS fixes was analysed as a 'choice' of whether to stay or travel, and where to choose as the destination. The choice set was defined as the home range, and five randomly generated possible destinations outside the home range. As we had too few journeys to generate a probability distribution, these 'available' possible destinations were defined using these five randomly placed sites the size of the average area-restricted destination within a 12.5 km buffer around the home range (the longest journey of a cat during this study). For cats that travelled to a destination in any month, the destination was added to the choice set and marked as chosen, even if the cat was not there for the whole month. The areas and shapes of home ranges and destinations were defined from a kernel density estimate of all suitable fixes using smooth cross validation, around a 95 % isotope.

To determine predictors of travel in a spatially and temporally dynamic landscape, we measured landscape features relevant to cats for each month. Fire extents were mapped using monthly Landsat 7 remote-sensing imagery available from the US Geological Survey (2011–2013). For each burnt area, we assigned the date of burn, the intensity (intense = 100 % tree scorch and no ground cover remaining unburnt, or mild = all other fires). Fire was classed by intensity in binary variables at one, three, six, nine and twelve months since fire, relative to the date of each GPS fix. Regions were divided into relative prey abundance based on average number of small mammals caught per year per area, from an annual dataset (Legge, Australian Wildlife Conservancy, unpublished data). We also calculated percent cover of riparian habitats, known to be important to cats (Chapter 3). The percent of each habitat feature was measured for the home range and five possible destinations for each month of cat movement data. Standard case-control logistic regression models were implemented in R v. 8 (R Development Core Team 2008) using the 'survival' library (Therneau 2014), with a separate model for every combination of variables. These models were compared within an information theory framework to select the most parsimonious model.

To determine whether journeys consisted of directed movement that efficiently reached a destination, we compared each actual journey against 100 simulations of correlated random walks. We detected significant correlation in distances travelled between successive fixes using Jlung-box tests (Turchin 1998), where cats were more likely to move greater distances if previous step lengths were longer and turn angles were shorter. This bias was incorporated into the selection of random step-lengths. Each simulation used the same number of segments as the corresponding journey, and step-lengths and turn angles were drawn from the same probability distributions as the actual journeys. We counted how many of the 100 simulations reached the destination, and compared this against observed values using an analysis of variance test. To determine whether routes taken were more direct or tortuous than expected, we calculated the Fractal D (Nams and Bourgeois 2004) for each journey; direct distance between start and finish divided by the distance of route travelled. We also compared the bearing of the first three segments of travel against the bearing of destination.

We measured length of time at destination against the months since the intense fire, season, prey density at destination. Linear models were fitted to every combination of the above variables. Time at fire was log-transformed to fulfil assumptions of normality. Models were compared within an information theory framework.

Results

We studied movements of 32 cats (25 males and seven females) using GPS tracking between 2010 and 2013 in the Kimberley region of north-western Australia, acquiring a total of 121 cat-months of movement data. Movement paths of cats were profiled into three types: (i) within home-range movements, (ii) long-range journeys, and (iii) area-restricted movements at a destination (see Methods). We identified eleven clear instances of long-distance journeys, ranging from two to more than fifty days at a time. Cats journeyed up to 30 km away from their home ranges, but all area-restricted movements at distinct destinations were within 12.5 km of the home range. Eight of the eleven expeditions involved arrival at a distinct destination, defined as a site where a pattern of area-restricted search was initiated (see Figure 1). One cat died at its destination, so we cannot separate this travel from dispersal movements. Another was initially caught and collared at what we believe was its destination, not its home range. Its pelage matched that of a cat from 12 km away, who was known from a series of infrared camera records at that site over two years. It returned to that site after one month of GPS tracking. All journeying cats were adult males ranging in weight from 3.2 – 5.1 kg.

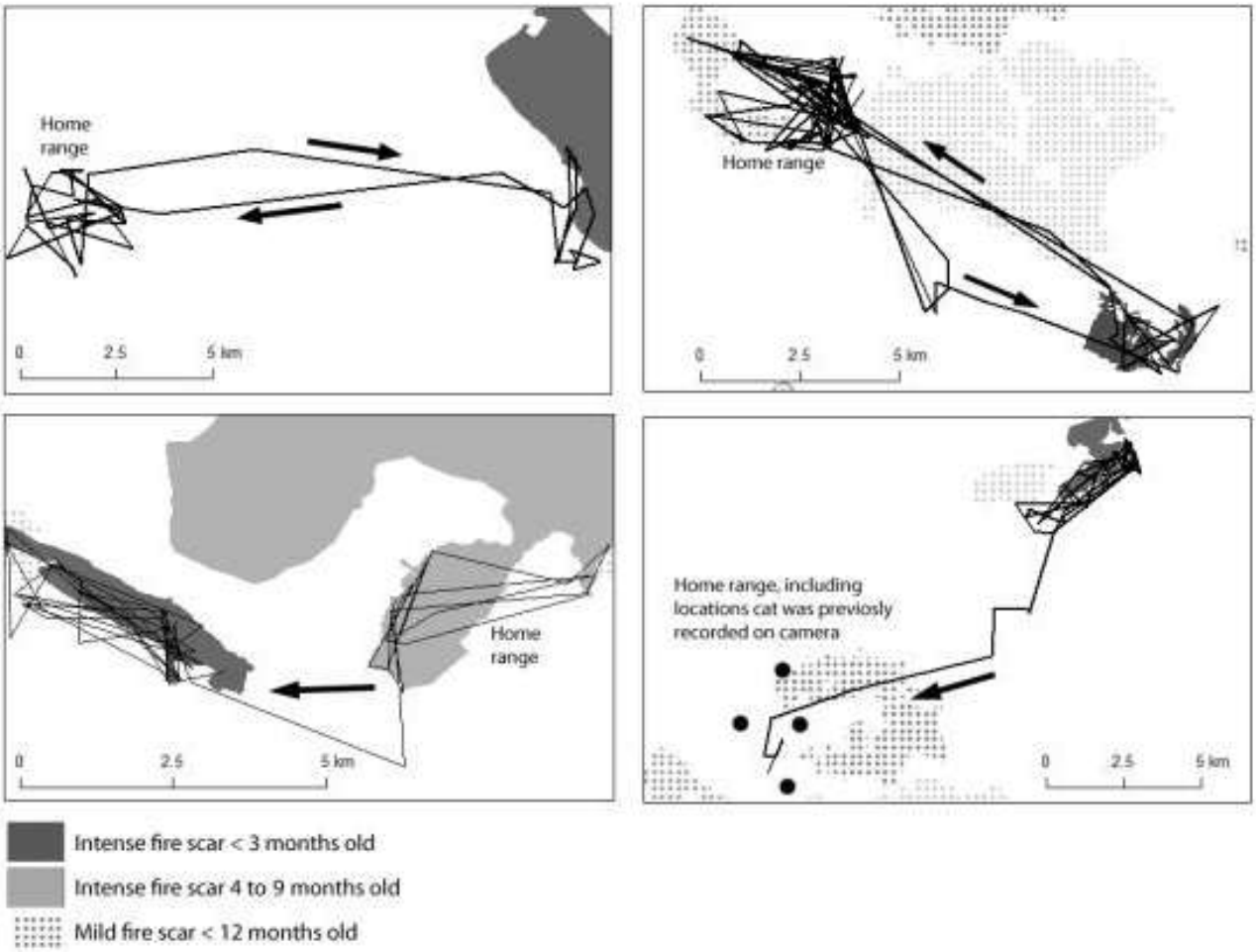


Figure 1. Examples of four of the eight extra-territorial travels to intense fire scars by cats.

Because cats preferentially use parts of their home ranges recently burnt at high intensity, we examined the role of fire in the surrounding landscape in eliciting long distance cat journeys. We created 480 discrete-choice models estimating the likelihood of a cat staying within its home range or traveling up to 12.5 km distant from its home range (the maximum distance of any destination from a home range) for any month, and measured fire and environmental variables. The most parsimonious model (Akaike weight = 0.58 and AICc of 12.9, compared to only other model in choice set with an Akaike weight = 0.21 and AICc of 13.59 for the next highest model) demonstrated that cats had a very strong fidelity for their home range, but that selection for recent intense fire-scars within 12.5 km was even stronger. Both variables had large effect sizes, with a home range coefficient of 11.3 ($z = 2.75$, $P = 0.006$) and an intense fire scar coefficient of 21.04 ($z = 2.54$, $P = 0.0112$). The model itself was significant (Wald test = 7.97, df = 2, $P = 0.018$), predicted cat selection in all but one of the 126 choice sets (that being the cat that travelled to the edge of a fire scar instead of inside it,

top right in Fig. 1). Other habitat variables did not improve model performance. For example, no cat travelled to a mild fire scar, even though 22 cats had the option of doing so. Destination ranges contained far more intense fire scars compared to the surrounding landscape, consisted of between 43 % and 96 % against 2 % to 27 % in the surrounding 12.5 km buffer. Of 12 cats that were monitored during periods when intense fire-scars covered more than 1 % of the area within a 12.5 km radius, eight set out on journeys to visit a fire scar. Two of the non-travellers were female that appeared, on the basis of infra-red camera images, to be lactating at the time. Therefore, 80 % of adult male cats that could have journeyed to a fire did so.

Once cats reached their destination, their duration of stay was on average 15 days, but increased with recency of the fire (Figure 2). From a choice set of three, the linear model with the lowest AICc (26.1 vs 28.4) and highest Akaike weight (0.58, vs 0.31 and 0.11) contained the single variable time since intense fire log transformed (value = -0.34, t = -3.8, P = 0.009); the model was significant (F =14.15, df = 6, P = 0.009; R^2 = 0.7). Season and prey density did not feature in the top candidate models.

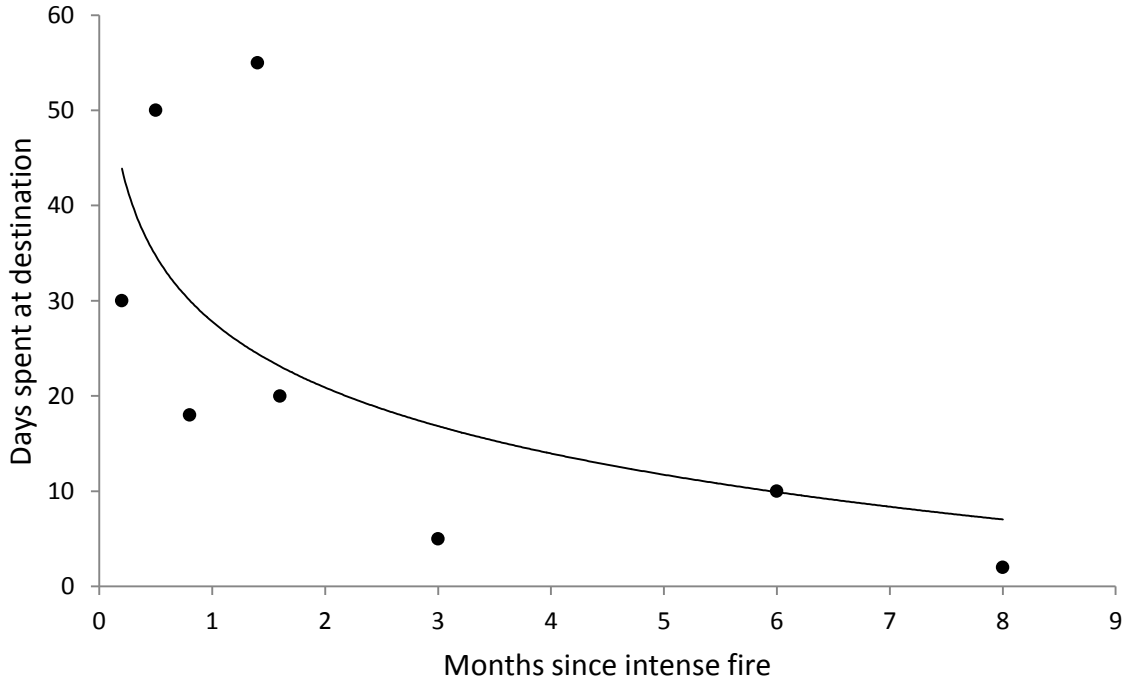


Figure 2. For cats expeditions to an intense fire scar, the duration of their visit in days is compared against the months since an intense fire at the destination.

To determine whether cats' journeys were purposefully directed towards intense fire scars, we compared each actual journey with 100 correlated random walk simulations using the same number of segments, and probabilities of turn-angles and distances. Compared to actual journeys, the simulated random walks reached an intense fire scar far less frequently (11 % of walks reached the fire, $F = 459$, $P < 0.001$), had a far lower tortuosity (Fractal D of 0.7 vs 0.31, $F_{1,8} = 26.4$, $P < 0.001$), and were less likely to begin in the direction of a fire scar ($F_{1,8} = 33.45$, $P < 0.001$).

Discussion

This is the first report of long-distance expeditions by a terrestrial mammalian predator to spontaneous and unpredictable pulses of prey availability. Feral cats made directed movements over long distances to intense fire scars, even though the animals otherwise held partially exclusive home ranges (Liberg *et al.* 2000, Chapter 2). Although the number of recorded journeys was small (11), the consistent destinations and strongly directed character of the movements make these data compelling. Even though all travelling cats were male, we do not believe these journeys had the objective of finding mates. The area-restricted searches that were initiated at destinations were at too large a spatial and temporal scale to be consistent with mating. While 80 % of the male cats exposed to an intense fire within 12.5 km of their home range journeyed to it, none of the 22 cats with a mild fire within 12.5 km journeyed, probably because such fires leave pockets of unburnt grasses that can provide refuge for prey and make hunting less profitable for cats (Banks *et al.* 2011; Leahy *et al.* 2014). We suggest that cats make these journeys to intense fire scars to take advantage of short pulses of high prey availability, where no such refuges remain (Birtsas *et al.* 2012, Chapter 3). Prey of feral cats (e.g. rodents) benefit from grass cover for protection from predators, and the complete loss of such would create ideal hunting areas for predators(Crowner and Barrett 1979; Leahy *et al.* 2014; Morris *et al.* 2011).

These long-distance journeys by cats create sudden dramatic increases in density of cats at fire scars, and could have an aggregate effect of driving down the density of small mammals over whole landscapes. We can estimate the likely local increase in cat density at fire scars produced by cats' journeying from the surrounding landscape. Considering a hypothetical fire of 100 km^2 (see Figure 3, **A**), in an area with a density of 0.17 cats per km^2 (Chapter 2), half of which are male, and assuming that 80 % of those would travel; that gives a total of 25 cats whose home-range adjoin the fire scar and an extra 70 cats within 12.5 km of the fire scar that are likely to visit it (see Figure 3, **B**). Given that expeditions were on average 15 days long and within a nine-month post-fire period (Figure 2), we would see on average four extra cats hunting within the fire scar, peaking with the months after fire (Figure 3, **C**). This would create substantial increases in cat density at fire scars, and corresponds with both the four-fold increase in cat activity and twenty-fold increase in small mammal predation rates recorded after a fire by Leahy *et al.* (2014). This estimate demonstrates how a relatively low

population density of cats (0.17 km^{-2}, Chapter 2) can have a major impact at a landscape scale, if fire regimes are not managed appropriately.

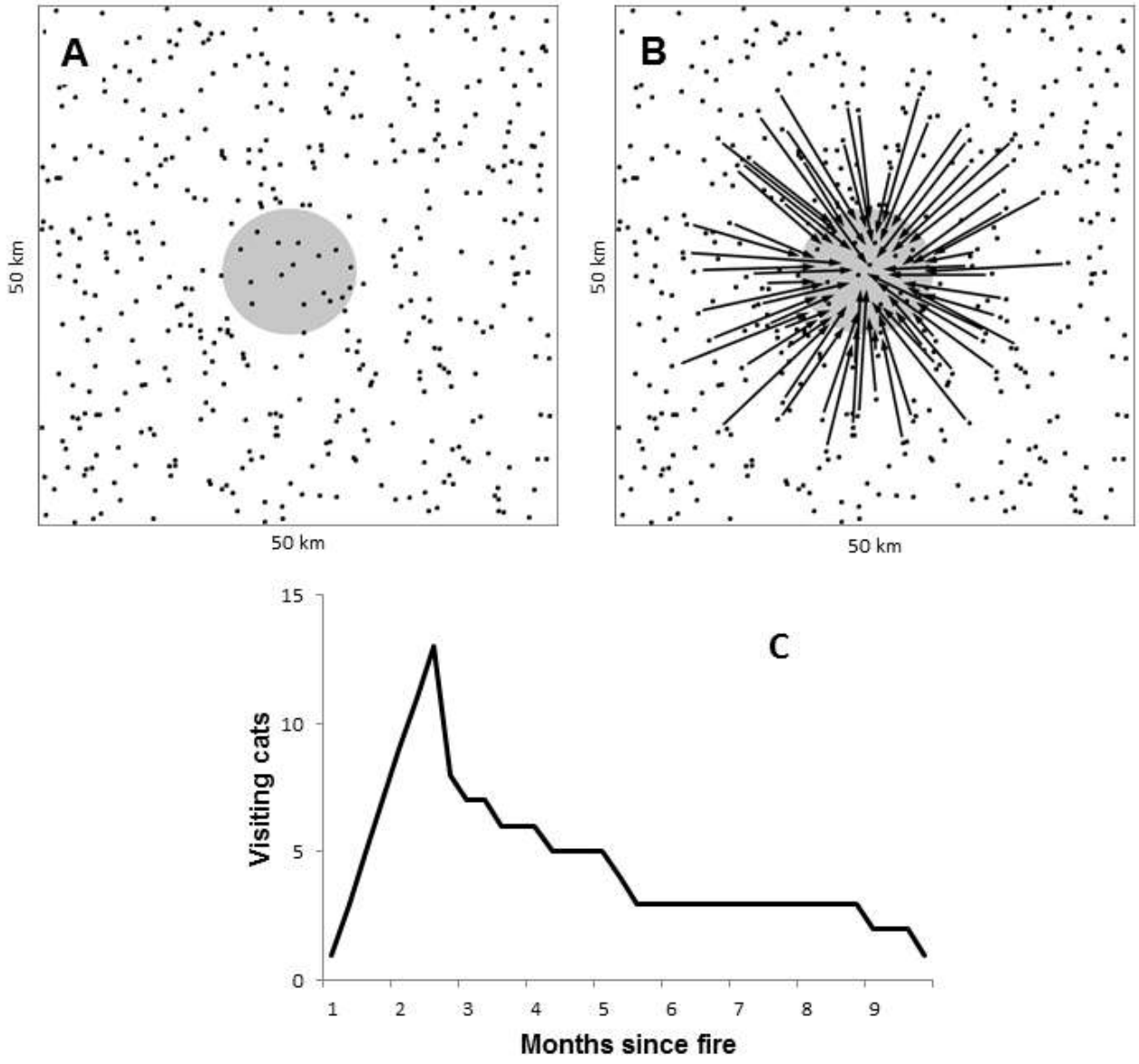


Figure 3. Simulation of localised cat density increases after an intense fire over a 50 × 50 km area, considering an intense fire of 100 km^2 and cat density (grey dots) in the study area of 0.17 cats / km^2 (**A**). As 80 % of males (40 % of total) would make expeditions to the fire scar, then 70 would do so (**B**). The number of simulated cats at the fire scar at any time since fire is presented in (**C**), based on Figure 2.

This study reveals an advanced spatial awareness in cats, beyond the area with which they are likely to be familiar from routine home-range movements. Although cats could have visited

these destinations before we placed GPS collars on them, they could not have known there would be a pulse of prey availability after an intense fire from memory of prior visits alone. They could have detected fire scars by either the smell of ash, or by observing the glow of fire from a distance. However, there was a time lag of at least five days between fire and journeys (average 73 days), so the smell of smoke or fire glow could not have been used as a direct guide for navigation. Instead, the cats would need to have retained the memory of the direction of their cues for days and up to several months before they embarked on their journey. The accuracy of some of the return trips demonstrate exceptionally large spatial scales for their mental maps, and suggest that the scale of spatial and temporal memory demonstrated in experimental settings (e.g. Dumas 1992; Goulet 1996) is only a small fraction of what cats are capable of comprehending.

Two of the greatest threats to wildlife globally are intensifying fire regimes and predation by invasive predators, and our documented interaction between these has major implications for conservation (Brook *et al.* 2008). In general, fire regimes are intensifying due to anthropogenic land-use change (Russell-Smith *et al.* 2003), invasions of exotic flammable grasses (D'Antonio and Vitousek 1992; Pausas and Keeley 2014), and global warming (Bradstock *et al.* 2014; Westerling *et al.* 2006). The latter would have the most profound long-term impact, as rainfall variability and hence extreme fire conditions will increase in all modelled scenarios (Flannigan *et al.* 2013). For wildlife, this means that not only will animals have to withstand the direct effects of these fires (e.g. Leahy *et al.* 2014; Morris *et al.* 2011), but potentially up to a five-fold increase in predator density as individuals from elsewhere come in to hunt the exposed animals. Our new understanding of the behaviour of feral cats provides even stronger grounds for reducing the frequency and extent of intense fires wherever possible.

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CHAPTER 5

Hunting behaviour of feral cats in a tropical savannah, revealed by animal-borne video-collars

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Target journal: *Journal of Applied Ecology*

Feral cat eating western chestnut mouse *Pseudomys nanus*

Abstract

Predation by invasive predators is a major threat to endangered wildlife. Unfortunately, there are many gaps in our understanding of this process due to the difficulties in observing predation events. Using small video cameras, we address three such knowledge gaps; i) kill rates of feral cats, ii) whether predation impacts are a function of space and/or time, and iii) variation of predation success between different microhabitats (open areas, dense grass and complex rocks).

We deployed modified GoPro video collars on 23 feral cats, and acquired 98 hours of footage of cat behaviour, and 101 hunting events.

Kill rates of feral cats were 7 per day, and 30 % of prey were not eaten. Predation rates were a function of space, that is, the further a cat travelled, the more hunting events were recorded. Hunting success was highly dependent on microhabitat structure, significantly increasing from 17 % in habitats with dense grass or complex rocks to 70 % in open areas.

Our results confirm that feral cats impose high predation rates, and conduct surplus killing. Predation rates were a function of space, so studies investigating the impacts of cats should assess their spatial ecology, not time spent in different areas. The greater kill rates in open micro-habitats has broad implications for management of macro-habitats, as it demonstrates that maintaining vegetation cover can protect species from cat predation.

Introduction

Predation is a dominant driver of prey population dynamics and the behaviour of prey. Shifts in predator-prey interactions can cause extinction of prey populations (Savidge 1987), with cascading impacts for entire ecosystems (Ripple *et al.* 2014). The strength of the effects of a predator on a prey population is governed by the size of the predator population relative to the prey, the availability of alternative prey, the preferences of predators for particular prey, and the hunting success of individual predators. While determining the size of predator populations might be straightforward, measuring hunting preferences and success is far more difficult, especially for mammalian predators. This is largely due to the difficulty of directly observing the behaviour of mammalian predators without disturbing either the predator or prey and thereby altering their behaviour. Also, when direct observation is possible, it is typically biased to locations of high visibility. Methods such as snow-tracking can partially overcome these problems (Helldin *et al.* 2006; Husseman *et al.* 2003), yet this method is limited to certain ecosystems. Predation events can be determined using GPS tracking of large carnivores that spend long periods at a kill (Hebblewhite *et al.* 2005; Mattisson *et al.* 2011), but predation of smaller prey with short consumption time will often be missed. A promising alternative solution for documenting hunting preferences and success is offered by animal-borne video-cameras (Moll *et al.* 2007).

Animal-borne video cameras have been extensively used to measure predator behaviour and kill-rates in aquatic ecosystems (Arthur *et al.* 2007; Heithaus *et al.* 2002), as the large size of some marine predators and the neutralising effects of buoyancy on weight of animal-borne cameras enables large camera packages to be used. Recent advances in miniaturising video cameras have allowed their deployment on terrestrial animals without significantly affecting behaviour (Moll *et al.* 2009), and provide an opportunity to directly observe predation from the predator's point of view. For example, small packages have been created for the study of predation rates by domestic cats *Felis catus*, taking advantage of the fact that the ease with which the animals can be handled means that batteries can be replaced frequently, so that small batteries are feasible (Loyd *et al.* 2013). Deploying comparable cameras on free-living mammalian predators in terrestrial systems remains a major challenge.

Predation by feral cats is a major ecological threat to small vertebrates worldwide (Denny and Dickman 2010; Loss *et al.* 2012; Medina *et al.* 2011; Woods *et al.* 2003). Woinarski *et al.* (2014) identified predation by feral cats as the single greatest contemporary threat to native mammals in Australia. This problem may currently be particularly severe in northern Australia, where there is evidence that feral cats are causing severe population declines of native small mammals (Fisher *et al.* 2013; Frank *et al.* 2014; Woinarski *et al.* 2011). Feral cats occur at low density in the savannas of northern Australia (Chapter 2) and they are wary and therefore extremely difficult to observe. The lack of information on the hunting behaviour of feral cats, and the kill-rates that individual cats are able to accomplish, means that we have very little capacity to predict or model the impacts of feral cats on populations of vulnerable prey, and to determine whether particular landscape features (some of which are created by human manipulation of the environment) aid or hinder hunting success.

The demographic impacts of predation by cats cannot be accurately measured without knowledge of kill rates. While these can be inferred from stomach contents, the period of hunting represented by a stomach sample can only be guessed, and many food types, such as bird eggs, are difficult to detect in stomach contents. Also, stomach contents do not register surplus killing, where prey are killed but not eaten. Surplus killing has been recorded in house cats (Barratt 1998; Loyd *et al.* 2013), and cats on islands with abundant food (Peck *et al.* 2008), yet we have no evidence of surplus killing by feral cats in Australia (Short *et al.* 2002). Surplus killing could cause large increases in kill rates, with profound effects on prey populations (Kruuk 1972).

Another gap in information on cat hunting is that most studies on the impacts of feral cats assume that areas of greater activity correspond with highest predatory impacts (Barratt 1997; Brook *et al.* 2012, Chapter 3; Jones and Coman 1982; Kennedy *et al.* 2012; Moseby *et al.* 2009). This assumption has never been investigated nor substantiated. We do not know whether cats hunt all the time, or only during specific bouts of hunting activity (e.g. Bailey and Thompson 2006). Also, we do not know whether hunting impacts are defined by space use, time, or a product of the two. This is especially important to studies of habitat use by cats, as different sampling methods and analyses are sensitive to space and/or time. For example, if an animal moves fast and far over habitat A, but slow and short over habitat B (see Figure 1), different analysis would come to different conclusions of preference. In this

example, an analysis of presence (e.g. number of cameras detected on) would show a preference for habitat A, while an analysis of location data at fixed time intervals (e.g. telemetry) would show a preference for habitat B (Buskirk and Millspaugh 2006). If hunting is represented by space use, then only the former analysis would capture the impacts on prey. This would be reversed if hunting activity is proportional to time. Considering the importance of the conclusions of the afore-referenced papers for management, this requires further investigation.

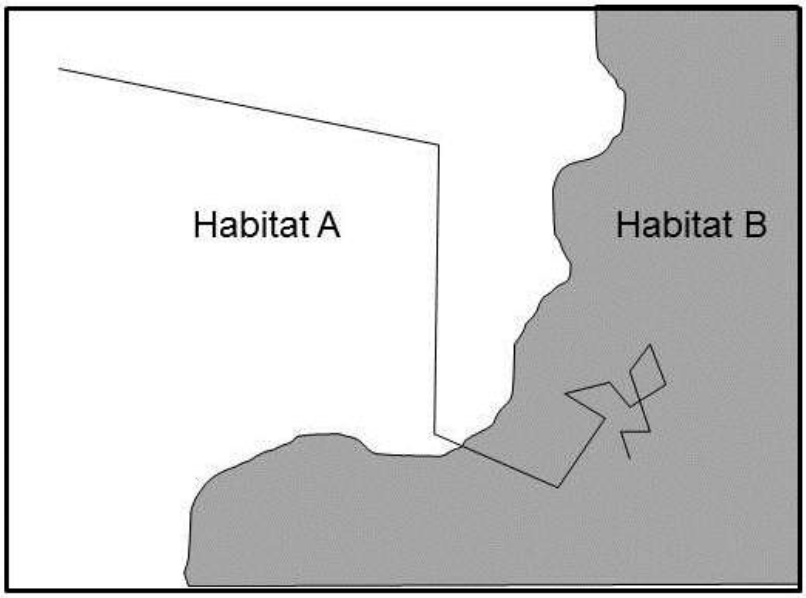

Figure 1. Example movements of a cat through two habitats (A and B) at set intervals of time. If space was considered, the cat would have greater impacts on habitat A. If time were considered, there would be greater impacts in habitat B.

The influence of landscape features in either aiding or hindering cat hunting is virtually unknown. In particular, we do not know whether features such as dense vegetation or rocks enhance or inhibit hunting success. Hunting by felids is typically a four-step process, involving detection, a stalk/ambush, pounce and kill. Dense vegetative cover might be of benefit to the cat by enabling a camouflaged stalk or ambush (Hopcraft *et al.* 2005; Lone *et al.* 2014); on the other hand, dense vegetation could hinder the pounce and kill steps by providing refuge for prey (Toland 1987). All studies on the influence of vegetation on

predation either come from large felids (e.g. lions *Panthera leo*; Hopcraft *et al.* 2005; Loarie *et al.* 2013) or use inferences from broad patterns of prey mortality in different habitats (Conner *et al.* 2011; Moreno *et al.* 1996). Understanding how vegetation structure affects the hunting success of cats is essential if we are to determine whether management of vegetation can change the impacts of cats on populations of vulnerable prey species.

In this study, we first show that animal-borne video cameras can document the behaviour and hunting success of feral cats, even in cases where footage is acquired within six hours of release from capture. First, we document the activity budgets of feral cats, Then, we use video footage to address each of the knowledge gaps discussed above, that is, to:

(i) measure kill rates accomplished by free-ranging feral cats, and test for surplus killing;

(ii) assess whether predatory impacts were a function of space, time, or both. The time spent moving (a proxy for distance covered) will be compared to the number of predation events. If impacts are a function of space, we would expect a strong positive correlation with an intercept around zero (i.e. no movement = no predation impacts), whilst for time we would expect a weak correlation and an intercept of more than zero (predation impacts relate to where cats spend the most time);

(iii) compare the hunting success of cats in contrasting open and dense vegetation.

Methods

Study area

The study was conducted on two properties in the central Kimberley of north-western Australia (17°01'S, 126°01'E), one managed for commercial cattle production (Glenroy, 1455 km^2) and the other a wildlife sanctuary managed by the Australian Wildlife Conservancy (Mornington Wildlife Sanctuary, 3225 km^2). Vegetation is characterised by savanna woodland with a perennial grass layer, dissected by riparian vegetation along the edges of creeks. The climate is classified as tropical monsoonal, where the majority of the annual rainfall (~600 mm/year) falls between December and April. All large introduced herbivores (cattle, horses, donkeys) have been removed from a 403 km^2 fenced section of Mornington since 2005 (Legge *et al.* 2011).

Camera design

Two different types of video camera collars were used, each with different methods of turning on to record video: manually or by remote UHF. All collars used a GoPro Hero 3 White camera, with after-market modification. Cameras had their infra-red filter removed, infra-red LEDs placed next to the lens (920 nm, with no visible light emission), an additional battery attached (20 g, with 1300 mAh), and carried a separate VHF beacon (Sirtrack, Havelock, New Zealand) (see Figure 2). Cameras turned on via UHF had a UHF remote chip attached, triggered with 433 mhz remote (Cam-do.com). All components were packaged together on a collar, and outer-coated in two layers of epoxy resin. The finished collars weighed 120 − 140 g, with payload dimensions of 65 mm x 35 mm x 43 mm. No package weighted more than 4 % of cat body mass. Collars were able to record 4 − 6 hours video.

Figure 2. Equipment used to create GoPro video collars (above), and finished product (below).

Deployment

Cameras were deployed on cats that had previously been captured for a study on habitat selection (Chapter 3), and had been carrying a GPS collar weighing 110 g for at least a month (that is, they were accustomed to wearing a collar of similar weight). Each cat was re-captured with the assistance of muzzled dogs trained to locate and chase them up a tree. Once treed, cats were sedated with a dart containing the sedative Zolotil at a rate of 0.5 cc / kg shot from a Pnue-Dart X-calibre $C0_2$ dart-rifle, then caught in a sheet stretched between two people as they fell from the tree. The GPS collar was removed and the camera-collar attached, and each cat was released at point of capture once the sedative had worn off (4 − 6 hrs later). In 14 deployments, cameras were turned on just before release. To account for the possibility that behaviour immediately after release was abnormal, on nine deployments we used cameras with a switch that could be activated remotely 2 − 10 days after capture. In such instances, we either approached quietly to 100 m and activated the camera via UHF remote, or used an automatic switch that was placed within the cat's home-range, which activated the camera when it came within 100 m of the station. Cats were re-caught 7 − 30 days later using the same methods to retrieve cameras and download footage.

Footage review

After cats were recaptured and collars retrieved, footage recorded pre-release was discarded. Post-release footage was scanned and classified into seven behaviour states:

- Sleep: No sign of consciousness, only occasional shifts of posture
- Rest: No change of position, but signs of alertness and movement.
- Grooming: Licking fur or scratching
- Drinking
- Walking: steady walking of less than two steps per second
- Running: vigorous movement of more than two steps per second
- Hunting: Any behaviour where a cat appeared to have detected prey, usually characterised by a still period of stalking followed by a pounce or prey retrieval; however, some other unambiguous prey hunting behaviour was witnessed (e.g. cat walking up to birds eggs and eating them).

In classifying behaviour, brief switches in behaviour (states that lasted for less than 10 seconds, before reverting to the previous behaviour) were not recorded, because this level of detail was considered unnecessary. The first 30 minutes post-release was discarded, as cats were generally running away. To test for other distortions of behaviour due to capture and release, we compared the proportion of each behaviour from footage acquired less than eight hours to that obtained from cameras remotely activated more than 2 days post release using a MANOVA (R Development Core Team 2008).

All successful and unsuccessful predation events were examined in further detail. We recorded the behaviour state (as above) of the cat at the time the prey was apparently detected, whether the cat initiated a stalk or pounce, diel period (day, night or 1 hr either side of sunrise or sunset), the species of prey where possible, success of hunt (whether the prey was killed), details of prey consumption, and micro-habitat. Micro-habitat was recorded for the area of the stalk, and approximately 50 cm around the point of predation event, based on footage from the camera. For both, microhabitat was divided into three categories; *open* (little/no grass above 10 cm, no rocks with crevices or caves), *grass tussocks* (any grass above 10 cm) and *rock area* (rocks with noticeable crevices or caves). Only microhabitat could be considered, as nocturnal footage was limited to the area illuminated by the LED in front of the camera (~1 m). A demonstration of how microhabitat was assessed in provided in Appendix 2.

To answer aims (i), (ii) and (iii), we conducted the following analyses:

i) Analysis of kill rates

To measure kill rates, we calculated average hunting per day as the number of kills for each deployment, and presented this as kills per day. Animals killed but not consumed we considered as surplus killing.

ii) Predation impacts against movement

To determine whether predation impacts of cats were a function of space and/or time, both successful and unsuccessful events were considered. Time spent hunting but not moving was excluded from each hour, so if a cat only rested and hunted, that would count as zero movement. For every hour of footage we compared the time spent moving (a proxy for distance covered) against the number of predation events. Both variables were square-root

transformed to assume normality. As some individual cats spent more time hunting than others (Churcher and Lawton 1987; Loyd *et al.* 2013), data were analysed using a linear mixed effects model (Pinheiro *et al.* 2014) with individual cats as the error term.

iii) Predation success and habitat

To measure the influence on predation success of diel period, stalk microhabitat, and prey location microhabitat, we created multiple generalised linear models with a binomial form. Instances where food was acquired but no stalk or pounce was initiated (e.g. eating birds eggs) were not considered in this analysis. We did not include identities of individual cats as error terms, as unlike the time spent hunting, variation in hunting success between individual cats contributed very little to the overall variation (< 4 %). Models were created with each variable and their combinations, and we determined which variables best modelled predation success within an information theory framework, calculating model weights and the relative importance of variables on the entire model set included in the analysis.

Results

From 23 deployments of video collars on 13 individual feral cats between 2012 and 2014, we acquired 98 hours of video footage. As we excluded the first 30 minutes of each deployment, 89 hours of footage were analysed. Of this 27 hours were in daylight, 62 hours at night-time. Cats spent the majority of their time sleeping, resting or grooming: these activities contributed to 66 % of all footage obtained (see Fig. 1). There were no significant differences between behaviours less than 6 hours and more than 24 hours post-release ($F_{1, 62} = 1.788$, $P = 0.128$).

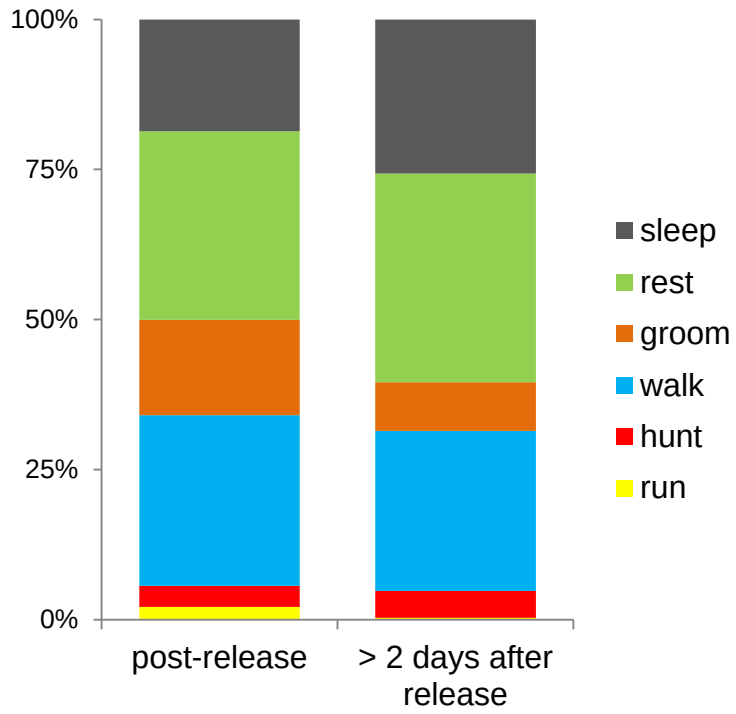

Figure 3. Activity budgets of feral cats during footage obtained within six hours of capture and release (left column, 61 hrs) and footage obtained more than 24 hours post release (right, 28 hrs).

i) Analysis of kill rates

From the 89 hours of footage, we recorded 101 hunting events, 32 of which were successful, equivalent to a rate of seven animals killed per 24 hours per cat. Eleven different prey species were identified. Frogs comprised 44 % of killed prey (see Table 1). Frogs were eaten in only 50 % of kills, and so contributed only 22 % to the total number of prey items consumed. Appendix 2 presents many of these hunts.

ii) Predation impacts against movement

For every hour of footage, there was a significant positive linear relationship between predatory activity and time spent traveling (T = 3.15, 1 and 23 DF, P = 0.004), with individual animal as a random effect (st. dev = 0.19, res = 0.51). The intercept, drawn without the inclusion of the random effect of cat, goes through zero (Figure 4).

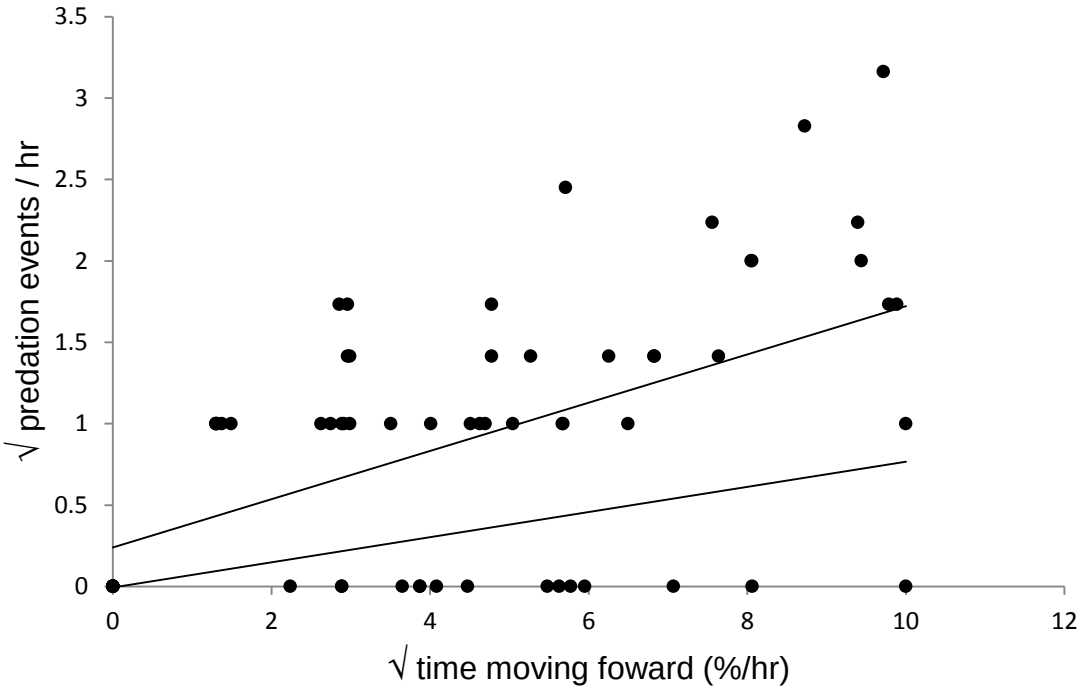

Figure 4. Relationship between the proportion of every hour spent moving forward (a proxy for distance travelled) against number of predatory events for each hour of footage, both square-root transformed (R^2 is 0.31).

Table 1. Prey species observed predated upon by feral cats, and details of body parts eaten.

Common name	Species	*N*	Details of consumption
Locust	unknown	1	eaten whole
Brown quail	*Coturnix ypsilophora*	2	eaten whole
Birds eggs	unknown	1	Only yolk eaten
Giant frog	*Cyclorana australis*	3	Stomach and legs eaten (1), uneaten (2)
Rocket frog	*Litoria nasuta*	2	eaten whole (1), head eaten (1)
Frog	various *spp.*	7	eaten whole (1), head eaten (2), uneaten (4)
Green tree frog	*Litoria caerulea*	3	stomach and legs eaten (2), uneaten (1)
Common rock rat	*Zyzomys argurus*	1	eaten whole
Western chestnut mouse	*Pseudomys nanus*	5	eaten whole (4), uneaten (1)
Gilbert's dragon	*Amphibolurus gilberti*	1	eaten whole
gecko	unknown	1	eaten whole
Western brown snake	*Pseudonaja nuchalis*	1	head chewed off, body half eaten
Shovel-nose snake	*Brachyurophis roperi*	1	eaten whole
unknown		3	
Total		**32**	

iii) Factors affecting predation success

Once cats had initiated a hunt by either stalking and/or pouncing, they were successful in 30 % of cases. Binomial generalised linear models were created for all combinations of predictor variables: microhabitat, behavioural and temporal, with success as the response variable. Both of the two top-ranked models (delta < 2, see Table 2) contained the variable of whether microhabitat was open (relative importance = 0.999), where cats were 2.7 times more likely have a successful kill if the prey located in open habitat (SE = 0.58, $Z = 4.7$, $P < 0.001$), and -1.68 times less likely to be successful if the microhabitat was grass or rock (SE = 0.33, $Z = -5.1$, $P < 0.001$) (see Figure 5). The other variable was whether the stalk was in the open and during the day (relative importance = 0.23), however this variable was not significant (SE = 1.3, $Z = 0.82$, $P = 0.41$).

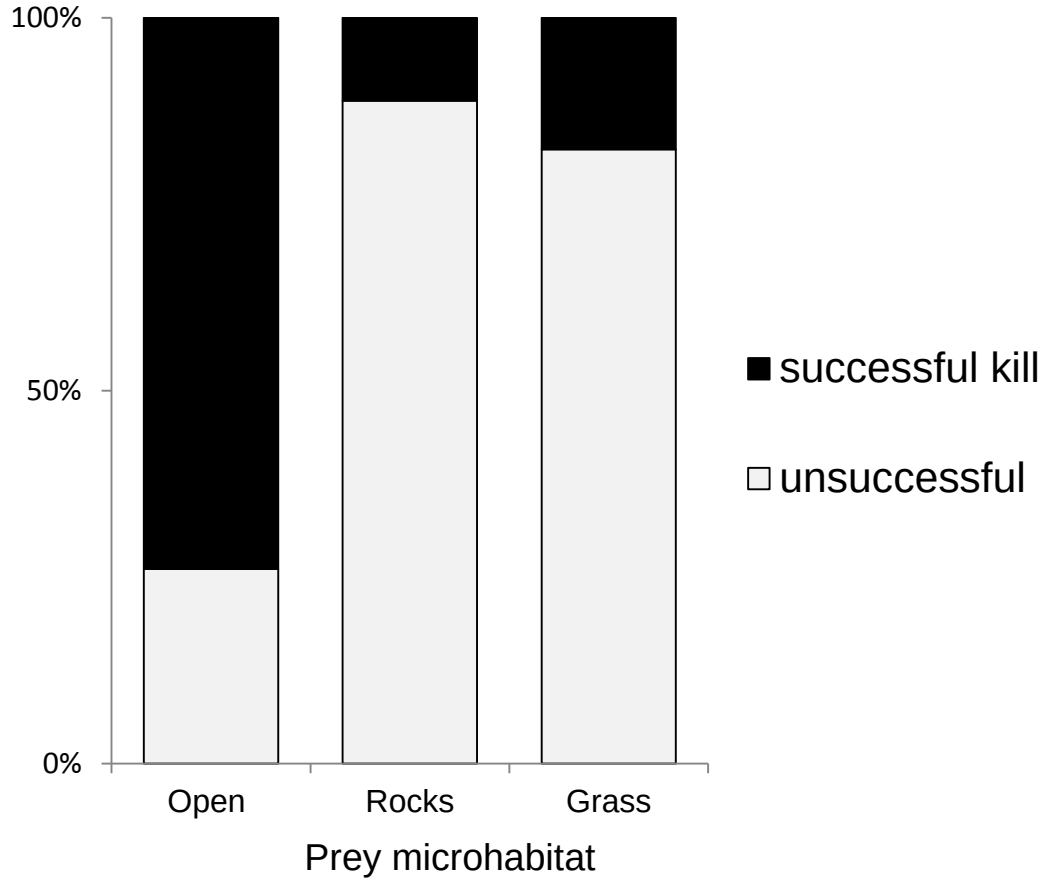

Figure 5. Portion of successful and unsuccessful predation events when prey was located either in the open (no grass cover over 10 cm), rocks, or grass tussocks.

Table 2. Details of the top candidate models, null model and global model. Other 11 models with delta > 2 not shown

Model	intercept	Cover open	Stalk open during day	df	logLik	AICc	Delta AIC	weight
1	-1.68	2.7		2	-43.644	91.4	0	0.5
2	-1.74	2.7	-0.2	3	-43.345	93	1.54	0.23
Global	-17.57			9	-42.027	104.2	12.8	0.001
Null	-0.84			1	-56.895	115.8	24.41	0
Relative importance of variable		0.99	0.23					

Discussion

Using small video cameras attached to collars, we were able to document and quantify hunting behaviour of feral cats in Australian savannahs. Cats were frequently observed predating upon native wildlife, with 101 events observed. Of these, 30 % were successful, similar to the 32 % success rate observed by the only other known such study on feral cats (Konecny 1987). Most hunting events were initiated whilst cats were moving. From footage of these hunting events, we were able to determine the importance of prey microhabitat as a refuge from cat predation.

Whilst the GoPro camera collars we modified were reliable and adequate for this research, they were not ideal. GoPro cameras are designed to maximise video footage quality at the expense of battery life, so the footage acquired per deployment was minimal (4 – 6 hours). Making the necessary modifications with battery extensions and infra-red capabilities is delicate and time consuming (~ 7 hrs per camera). Similar and more efficient cameras have been developed, such as KittyCams (Loyd *et al.* 2013), however, these were not available at the time to other researchers. Other small cameras that were commercially available either lacked the wide-angle lens, video quality, or memory storage capacities. There is enormous need for further development of such animal-borne video technology and for it to become more readily available. As we discuss below, even our limited length of footage was able to provide critical data on gaps in our knowledge of cat hunting dynamics.

i) Analysis of kill rate

We recorded a hunting rate of seven successful kills per day. This demonstrates that feral cats have a far greater impact on prey populations than domestic free-ranging cats. Loyd *et al.* (2013) found kill rates of just 0.34 animals per night using animal-borne video cameras, over 20 times less than our reported kill rate. Kill rate is likely to vary across different regions as it would be strongly related to prey availability, yet be constrained by the minimum number of prey needed for a cat to stay alive. Cats are known to kill even when sated (Adamec 1976), therefore their kill rate is likely to be much higher in areas of greater prey availability than the rate recorded in this study of 30 %. Our results suggest that inferring kill rates from stomach contents gives substantial underestimates, because at least 32 % of all recorded kills

were either not eaten, or only un-identifiable parts were eaten (e.g. frog intestines, or egg yolk).

We recorded 11 different species as prey of feral cats. The dominant prey killed by cats were frogs, contrasting with all other known studies of diets of feral cats in Australia, which detected few or no frogs (Denny and Dickman 2010; Loyd *et al.* 2013; Martin *et al.* 1996). This difference in results could be explained by the fact that few frogs were eaten whole and hard parts were often not consumed, in which case predation would not be evident from analysis of scats or stomach contents. Also, in the current study, many of the deployments were carried out in the wet season, when frogs are highly abundant even away from standing water. Snakes, ground-dwelling birds and small mammals were the other dominant prey species, similar to other studies. Interestingly, feral cats appeared adept at distinguishing between snake species. When the venomous western brown snake *Pseudonaja nuchalis* was eaten, the cat spent almost 10 minutes chewing off the head, which was then discarded, presumably to avoid ingestion of venom. However, the non-venomous shovel-nose snake *Brachyurophis roperi* was eaten quickly whole.

The proportion of animals killed and not eaten (29 %) constituted surplus killing. This has potentially worrying implications for kill rates in circumstances where prey are unable to avoid predation, as kill rates appear not to be limited by the food requirements of the cat. Such examples may include cats hunting small mammals after intense fires, where all ground cover has been removed (Conner *et al.* 2011; Leahy *et al.* 2014). However, all unconsumed prey bar one were frogs. Therefore, it is possible that the surplus killing recorded in this study was related to some special feature of frogs, such as low nutritional value, or unpalatability due to mild toxicity of substances produced by skin glands. Further video evidence will be required to assess the rate of surplus killing in other prey.

Using results obtained here, we can estimate the kill rates imposed by the cat population of the study area. Cat density over the two properties where we conducted this study is on average 0.17 adult cats per km^2 (SE 0.08). If each of these cats killed 7 animals a night, the total kill would sum to over 2 million native animals killed each year across the 4680 km^2 study area, making 1.2 animals killed per km^2 each night.

ii) Hunting during different behaviours

Cats were most likely to hunt while walking, and there was a strong relationship between distance travelled and number of predatory events. Also, when there was little movement, there were few predation events. This provides weight for the hypothesis that predatory impacts are largely a function of space, not time. In other words, the impacts of cats are related to the distance over which they travel, rather than the time spent in any given spatial unit. This highlights the need to incorporate behavioural states into studies of cat movements (Patterson *et al.* 2008), so that the influence of areas in which cats spend much time but with little movement is not inflated in analyses of the spatial distribution of predator pressure (Buskirk and Millspaugh 2006). These findings suggest that the distribution of predation can be inferred from data on movement and activity of cats (Chapter 3), although we defined space in this study only as time spent traveling, and did not measure any other spatial aspects like path tortuosity. Further research into relationships between predatory impacts and movement characteristics is warranted (Maletzke *et al.* 2008; Weimerskirch *et al.* 2007).

iii) Factors affecting predation success

Microhabitat had a strong influence on hunting success. Feral cats were over three times more likely to make a successful kill in open microhabitats versus grassy or rocky areas, once a prey animal had been detected. Grass tussocks and rocks are thus highly valuable in providing refuge for prey, and when present they protected against 80 % of observed predation events. This corresponds with other studies of small mammal mortality in northern Australia. Oakwood (2000) found northern quolls *Dasyurus hallucatus* living in rocky areas were twice as likely to survive than those in unprotected habitats, whilst Leahy et al (2014) found pale field rats *Rattus tunneyi* to be much more likely to be killed by predators if grass cover had been removed by fire. There are limitations in applying these data solely to small mammal predation, though, as the identity of the prey species from unsuccessful hunts is not known. We suspect that there were prey species-specific biases in predation success between microhabitats. For example, grass may not provide sufficient cover for larger animals (e.g. snakes) to evade predation as they would be more easily extracted.

While the influence of microhabitat in protecting prey was clear, it requires careful extrapolation to attribute these results to habitat types or conditions. As spatial movements of

cats were not recorded, we could not measure macrohabitat (e.g. whether the hunting was attempted in spinifex woodland or riparian forests), and were therefore unable test its effects on hunting success. A simple extrapolation could approximate this. We could estimate the success rate for a cat (where success is defined as killing a prey individual once it was detected) as the percent cover of grass and rock cover multiplied by the corresponding predation success coefficient (-1.7), then adding the percent cover of open substrate multiplied by its coefficient (2.7). If this were applied to habitats within our study area, it would explain why cats in our study area selected strongly for recently burnt grasslands with a high abundance of small mammals (Chapter 3). However, this does not take into account many other factors, and will need to be field-tested.

The patterns reported here, of ground cover and rocks protecting prey from feral predators, correspond with habitats that have retained threatened mammal species across Australia. It suggests why structurally complex habitats that have complete cover of grass and shrubs have retained threatened species extinct elsewhere on the mainland. One such example is the Gilbert's Potoroo *Potorous tridaetylus* at Two Peoples Bay (Sinclair *et al.* 1996), that was once widespread but now only persists in long-unburnt coastal heaths. If this pattern of greater predation success in open areas applies elsewhere in Australia, it would explain why native mammal extinctions were more prevalent in regions with more open habitats such as the arid zone (Johnson 2006; Smith and Quin 1996). These findings have clear implications for the conservation of species threatened by feral cats: management to maintain the cover and density of ground vegetation can be used to reduce the impact of feral cats and, perhaps, allow vulnerable prey to coexist with this predator.

Conclusions

The results from this study contrast with evidence obtained from larger carnivores. Kill rates are much lower for all recorded large carnivores, with lynx *Lynx lynx* as low as 0.1 to 0.3 per day (Mattisson *et al.* 2011) and lions at 0.4 per day (Orsdol 1984). Capturing prey is a much more intensive activity, and a single large prey can provide enough food for many days. Hunting may not only be a function of space use, as some larger predators either spend hours in ambush for prey (Hart *et al.* 1996; Orsdol 1984), or will only hunt during specific behaviours whilst moving (Maletzke *et al.* 2008). And when predators and prey are roughly

the same size, there are very different patterns between predation success and landscape factors. For example, dense vegetation assists hunting for most African large cats (Balme *et al.* 2007; Hayward *et al.* 2006; Hopcraft *et al.* 2005), as it enables camouflage during a stalk.

Alternatively, we anticipate most of the patterns observed here are likely to be applicable to other small predators, as most are opportunistic hunters and preferentially hunt prey much smaller than themselves (Gittleman 1985). This means that most would require high kill rates to acquire enough energy to survive (Carbone *et al.* 1999). Predation pressures would be a function of space, as few small predators are known to do protracted ambushes where they would be still for a vast amount of time (Gittleman 1985; Kitchener 1991). And patterns of decreased predation success in more dense grassy and complex rocky microhabitats are likely to be consistent, as their prey could move and take refuge in such areas yet the predators cannot. However, there is little evidence for this at present, and hopefully more researchers in other systems can have access to animal-borne video for deployment on other terrestrial predators and further our understanding of hunting dynamics.

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CHAPTER 6

Overall summary and discussion

I was able to make detailed observation of the ecology of cats *Felis catus*, and show how their population density, movements and hunting success are affected by fire and grazing regimes. Efficient and effective methods were developed for measuring density, catching cats to study their movements and observe their hunting.

By measuring cat densities at multiple camera-trap arrays across the central Kimberley, I showed that cat densities were low (around 0.17 km ^{2}) but stable and relatively uniform across the landscape. No relationship was found with either stocking or long-term fire histories. This is despite large differences (2-8 fold) in small mammal abundance related to these variables. This suggests that within those areas, prey were abundant but not necessarily available to cats.

I then investigated fine-scale habitat selection by feral cats in relation to fire, grazing and small mammal abundance, using GPS data obtained from 32 feral cats in landscapes with contrasting fire and grazing patterns. Cats selected areas with less grass cover, including areas that were heavily grazed or burnt by intense fire. However, they did so only in habitats that typically support high abundance of small mammals.

Not only were areas burnt by intensive fires selected by cats within the home range, but males would journey far outside their home ranges in order to hunt in such habitats. Eight such journeys of up to 12.5 km were recorded, representing 80 % of male cats that had an intense fire scar within that distance of their home range. The aggregate effect of these expeditions was to create temporary increases in cat densities at intense firescars, which would place much greater predation pressure on native wildlife in those places.
In open areas with scant grass or rock cover, hunting attempts by feral cats resulted in a successful kill more frequently than in closed areas. As fire and grazing simplifies the

structure of vegetation at ground level, it is reasonable to conclude that fire and grazing improve the success rate of cat predation.

Each chapter demonstrated one aspect of cat ecology, pointing to some manner of increased impacts on prey with intensified fire and grazing regimes. However, these need to be synthesized in order to estimate the magnitude of this change. I therefore used my results in a hypothetical scenario for a 50 km x 50 km area with an intense fire that covered 100 km^2. Assuming a density and spacing of feral cats as was found in Chapter 2 (0.17 km^{-2}), this entire area would support a population of 425 cats. The fire scar itself would contain the home-range centroids of 17 cats, and the home-range of a further 8 cats would be adjacent. Considering the degree to which cats selected for intense fire scars within their home range (Chapter 3), we can assume that visitation by cats to areas with an intense fire scar within their existing HR would double. Also, if we consider that 80 % of male cats living within 12.5 km of the edge of this fire scar would travel there (Chapter 4), this means another 70 cats would visit. The visits would take place for at least nine months after fire, with longer stays initially (within 3 months of fire), and shorter stays over time; however on average there would be about 4 additional cats at the fire scar in any week. And finally, the success rate of predation attempts by each cat would increase three fold due to the open-ness of habitat (Chapter 5). Combining these estimates, there would be a two-fold increase in resident cat visitation, four-fold increase in cat density, and three-fold increase in likelihood of a kill if detected, with the ultimate effect that prey would be subject to a 15-fold increase in cat predation.

In this scenario, movement of cats to fire scars might provide temporary relief from predation for small mammals at the home ranges of those cats, but because predation risk is lower in unburnt habitats this relief would not offset the increased mortality at fire scars. The increase in intensity of predation at fire scars is so great that it could lead to local extirpations of prey, such as small mammals, that are targeted by cats in those situations (Leahy *et al.* 2014). It is possible that if intense fires recur with sufficiently high frequency, these local extirpations could incrementally spread to affect large areas (Firth *et al.* 2010; Pardon *et al.* 2003b). If the pace of this process exceeded the potential for dispersal and local recruitment to re-establish populations of small mammals in the wake of intense fires, the result could be regional

extinction of many species of small mammals. A process such as this could explain the recent wave of small-mammal extinctions across northern Australia.

The effect of grazing by large herbivores on the magnitude of the impacts of cats is harder to discern, especially for their impact on small mammals. Cats' selection for grazed habitats was stronger during the day, but this is not when small mammals are most active. However, grazing by livestock produces a more open structure of ground vegetation, and my data showed that cats prefer more open areas to hunt it, and make more successful kills in open areas. Though my evidence is somewhat circumstantial, it does provide a potential mechanism to explain the results of earlier work in the same area that showed immediate increases in the richness and abundance of small mammals after removal feral herbivores (Legge *et al.* 2011b). There are several alternative mechanisms to explain grazing impacts. Large herbivores may affect the small mammals directly, by reducing food availability and hence fecundity, or trampling their burrows. Alternatively, there could be an interaction with fire, as cattle are known to prefer grass regrowth after fire, amplifying the impacts of intense fires that were discussed in the previous paragraph.

Implications for the northern mammal declines

The key point from this research is that the impacts of cats can vary dramatically with changes to fire, and possibly grazing regimes, despite a low cat density. Based on this, the cat-fire-grazing interaction is a strong candidate mechanism to explain the northern mammal declines. In this scenario, cats and small mammals coexisted for over 80 – 150 (depending on the region) years at stable equilibrium [1], where fires were small in scale, and grazing relatively light. However, the large shifts in fire patterns witnessed over the last 60 to 20 years, along with increased grazing pressure from cattle , horses, donkeys, buffalo, created an increasing frequency of pulses of high cat impacts, driving major population declines of native mammals, without necessarily an increase in cat populations. This interaction between feral cats, small mammals, fire and grazing fits in with most known investigations of small mammal responses to fire and grazing (Andersen *et al.* 2005; Kutt and Woinarski 2007;

[1] Not all native small mammals coexisted within this equilibrium, and it is likely that some species went extant almost immediately after European colonisation of northern Australia (Cramb and Hocknull 2010, Start *et al.* 2012)

Legge *et al.* 2011a; Legge *et al.* 2008; Woinarski *et al.* 2010). However, there are some anomalies to this pattern in northern Australia. Cats are present on Melville Island to the north of Darwin, but preliminary evidence suggests small mammals are not declining there with frequent fires (Burbidge and Manly 2002; Davies and Murphy 2014). Also, in northern Queensland successful suppression of fire and removal of cattle did not result in increases in small mammal abundance (Kutt *et al.* 2012). It is possible that these differences are due to variations in cat abundances, where certain thresholds create different outcomes. Landscape variations in cat density should hence become a further avenue for cat research in northern Australia.

That the cats-fire-grazing interaction is so strong does not mean that other factors are not important in causing decline of small mammals in northern Australia. Dingo *Canis familiaris dingo* persecution likely has had a role, because dingoes suppress cat numbers and/or behaviour, at least partially excluding them from certain habitats (Brook 2013; Leahy *et al.* 2014; Wang and Fisher 2012). Cane toads *Bufo marinus* are contributing to the decline of the northern quoll *Dasyurus hallucatus* by direct poisoning (Oakwood 2000), and this may apply to other carnivores as well (e.g. northern brush-tailed phascogale *Phascogale pirata*). Cane toads may also contribute to declines of native rodents like *Rattus tunneyi* (Ibbett 2010), via competition for burrows and food. Furthermore, how fire and grazing affect the trophic regulation of ecosystems as a whole is not understood (Radford *et al.* 2014).

Implications for Australia

My research also suggests the likely cause of mammal declines in the desert regions of Australia over the last 100 years. Whilst some of the critical weight range mammals went extinct soon after European settlement across the centre (Johnson 2006), many persisted in the period between the 1930s and 1970s (Burbidge *et al.* 1988; Finlayson 1935; Gibson *et al.* 1994; Ziembicki *et al.* 2013). Aboriginal people continued to live in the desert and carried out their burning practices, creating mosaics of small fire scars, until as late as the 1960s (Burrows *et al.* 2004). However, most aboriginal people had moved into settlements by the 1970s, and the fire regimes rapidly changed into a pattern of massive intense fires. Soon after, many native mammal populations became extinct. These changed fire patterns are often considered the reason for these extinctions by both scientists (Smith and Quin 1996) and

traditional owners (Burbidge *et al.* 1988; Ziembicki *et al.* 2013), yet the evidence is scant. I suggest that the change in fire regimes would have caused prolonged and increased predation impacts by cats (and possibly red foxes *Vulpes vulpes*) on critical weight range mammals. Whilst the contribution of this process compared to others factors (e.g. increase in cat density caused by the reduction in aboriginal hunting of cats) cannot be assessed, there is strong evidence that it was at least operating. This suggests the manner in which fire regimes should be considered in these ecosystems. It is not necessarily that fire-mosaics and 'pyrodiversity' in themselves are important. Instead, it is the size and frequency of intense fires that drive declines in combination with feral predators, and that such mosaics supress the spread of such fires (Bird *et al.* 2012). This would explain why few studies report increases in small mammals in areas with greater pyrodiversity (Parr and Andersen 2006), and why these patterns were not observed on arid offshore islands in the absence of predators (Short and Turner 1994). This highlights the importance of ongoing fire management throughout central Australia to protect the remaining few extant mammals.

This interactive threat is also likely to affect the fauna of southern Australia. It is possible that foxes, the dominant introduced predator of southern Australia, also have greater predatory impacts on native mammals after intense fires. Meek and Saunders (2000) found radio-tracked foxes appear to select for intensely burn areas, and Hradsky *et al.* (2014) found that foxes eat more native small-medium sized mammals after fire. Also, small mammal populations generally decline following intense fires (Arthur *et al.* 2012; Banks *et al.* 2011; Friend 1993; Green and Sanecki 2006; Sutherland and Dickman 1999). At present, refuges for endangered critical weight-range animals in southern Australia are either long-unburnt heathland (Sinclair *et al.* 1996) and rainforest pockets (Bennet 1993; Johnson 2006; Sinclair *et al.* 1996), suggesting that the reason for these species persistence is the continuous protection from predation provided by dense vegetation. This research highlights the precarious situation that these threatened mammals are in, as one intense fire could create a feeding frenzy of cats or foxes and increase their predation pressure dramatically.

This pattern of opening up of ground-layer vegetation increasing predatory impacts of small-medium sized carnivores would be applicable worldwide, however, does not seem to have as dramatic an impact on prey populations. Other studies in Europe and the Americas find that small-medium sized predator activity and predation impacts increase after intense fires

(Birtsas *et al.* 2012; Cunningham *et al.* 2006). As fire and grazing create at least temporary opening up of ground cover, most species of small-medium sized predators should have greater hunting success in such areas. Unlike in Australia, populations of small to medium sized mammals do not appear to be as threatened by such events (Conner *et al.* 2011; Fisher and Wilkinson 2005; Izhaki 2012; Morris *et al.* 2011).

I suggest a hypothesis as to why this pattern is more severe in Australia. The main difference between Australian versus Eurasian and American mammalian assemblages is the absence of placental predators (Order Carnivora) over most of Australia's evolutionary history. Wide-ranging and flexible predators such as cats and foxes appear to exert a greater predatory force on prey than Australia's predators such as quolls *Dasyurus* spp. and Tasmanian devils *Sarcophilus harrisi*, and one of the key evolutionary responses of small mammals of Eurasia and the Americas was to increase fecundity. The small terrestrial mammals of Australia have a comparatively lower fecundity, even within the rodents that occur on all three continents (Watts 1974). As Australian mammals did not evolve with the same predation pressure as Eurasian and American species, evolutionary traits that put more emphasis into survival in a nutrient-poor landscape were selected for. After feral cats and red foxes were introduced into Australia, their anti-predator traits, either physiological or behavioural, were no longer effective. The only factors that reduced predation rates to sustainable levels for most species was either a reduction of cat or fox densities (usually by the top-order predator dingo (Ritchie and Johnson 2009)) or the availability of cover in the form of dense low vegetation or complex rocks. The presence of dense low cover allowed some species to coexist with introduced species in some circumstances, namely the northern Australian savannas, semi-arid spinifex grasslands and southern heathlands. However, even momentary losses of cover with no nearby refuges (e.g. after intense fires) can drive these species to local extinction.

Global implications

This research demonstrates that two of the greatest threats to wildlife globally, intensifying fire and grazing, and predation by invasive predators, can interact to create even greater impacts. In northern Australia, much of the small mammal fauna was seemingly able to adapt to the introduction of an invasive predator, at least temporarily. However, this fauna could not remain stable with the interactive effects with intensifying fire regimes and greater

grazing pressures. When multiple threats affect whole landscapes, population declines may be so rapid that it denies animals a chance to adapt to any one threat (Brook *et al.* 2008).

One of the key implications for conservation is to reduce the frequency and extent of intense fires wherever possible. Globally, fire regimes are intensifying. The principle reasons are anthropogenic land-use change (Russell-Smith *et al.* 2003) and global warming (Bradstock *et al.* 2014; Westerling *et al.* 2006). In the context of reducing the impacts of fires, the most important consideration is to reduce the frequency and extent of intense fires, not necessarily any fires. Reducing intensive fires using many smaller controlled (i.e. mild) fires is a valid option, even if these fires themselves cause damage. For example, while Leahy *et al.* (2014) found a five-fold drop in survivorship of *Rattus tunneyi* after a mild fire, there was a 20-fold drop after an intense fire. Similar results have been obtained elsewhere (Firth *et al.* 2010; Pardon *et al.* 2003a), suggesting that in general, all fires enable greater hunting by predators, but intense fires are especially catastrophic. The trade-off must be made in the impacts of preventative fires against the threat of intensive fires

Cats are a major cause of population declines and extinctions worldwide (Loss *et al.* 2012; Medina *et al.* 2011; Woinarski *et al.* 2014). My research shows that even at low densities feral cats can be major threat to wildlife. They are more opportunistic and intelligent hunters than previously thought, in that they were able to find fire scars far outside their home-ranges to hunt. Also, their kill-rates are much greater than has been reported for domestic cats (Barratt 1998; Loss *et al.* 2012; Loyd *et al.* 2013), and wild cats are capable of surplus killing. Cats need to be managed for conservation. Unfortunately, one of the greatest difficulties in managing cats is that their behaviour, ecology and impacts are so varied across their range, and solutions that are effective in one place and time are not necessarily applicable elsewhere. For example, strategies for removing cats on islands, such as the introduction of cat-flu and intensive trapping (Nogales *et al.* 2004), are not applicable to managing cats around cities, where there is high resistance to disease and recruitment would be far greater than removal (McCarthy *et al.* 2013). It is critical to modify management strategies to the locality and conditions.

Populations of feral cats are very difficult to reduce over large scales. For removal of animals from wild populations to succeed in reducing abundance, the removal rate must exceed the

rate at which the population replaces removed animals by recruitment through reproduction and immigration. The high reproductive potential of feral cats means that a very large portion of the population must be removed, between 65 % and 95 % of the population per year (Hone 1999; McCarthy *et al.* 2013). Using current methods of direct control, detecting and killing the required proportion of the population to deliver an overall population reduction when at low densities is a virtual impossibility. Poison baiting may be an option for parts of Australia where risks imposed on native carnivores are low, however, such scenarios are rare (Paul *et al.* 2011) and low bait uptake by cats means that success of this method is variable (Johnston 2012; Johnston *et al.* 2011; Johnston *et al.* 2014; Moseby *et al.* 2009). No known feasible bio-control option has been suggested. Instead, other methods of reducing cat impacts on native wildlife will have to be considered.

This research suggests that in areas where cat density is low, cat impacts can be reduced by focussing on management of vegetation to increase ground cover. This could be achieved by supressing intense fires and reducing populations of feral herbivores. This would reduce the impacts of cats over large landscapes, especially if this management is focussed on naturally mammal-rich habitats, and suggests why fire management and cattle removal has had positive results in the central Kimberley (Legge *et al.* 2011a). A key question is how changes to vegetation structure influence predation in different habitats, and in areas where densities of feral cats are greater. This is where future research must be directed.

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Supplementary material

Appendix 1. Details on the creation of the dynamic grass cover map

To accurately measure grass variables in a landscape of constantly changing grass biomass, we developed a dynamic map that estimated grass cover at any given location and date. This involved creating a series of models of grass cover, derived from vegetation attributes measured at 768 plots. These plots were each 10 m^2, and spread across the study area. To encompass a full range of fire and grazing responses in grass growth, we used a stratified random sampling design with six plots placed in each grass community (see Table 1) and to each combination of mild / intense fire; in four time periods (up to 1 month post fire, 2 – 12 month post fire, 12 – 24 month post fire, greater than 25 months since fire; in grazed and destocked areas. This created a total of 96 plots per community.

At each of the 768 plots, we estimated the extent of grass cover at different heights by adapting a line-intercept method. First, dominant plant species were identified. Then, we inserted a 100 cm pole (diameter of 1.5 cm) vertically through the grass to the ground at 50 points in a systematic grid over the plot. The number of grass intercepts were recorded in height brackets of 0 – 10 cm (cat paw height), 11 – 30 cm (cat body height), and 31 – 100 cm (greater than cat body height). For each plot, we converted this into grass cover (% of poles with any grass intercept higher than 10 cm), dense grass cover (% of poles with 10 or more grass intercepts; typically the centre of tussocks), and grass biomass (total sum of grass intercepts). We considered grass cover relevant for cats to be that higher than their paws (~ 10 cm), and grass cover less than this would not assist their concealment or impair their vision. Therefore, cover was measured as the percent of poles with any grass intercept greater than 10 cm.

To determine values for grass variable (cover, dense cover and biomass) for any given location and date in the study area, models were derived from values for each plot and plotted against other spatial and temporal explanatory variables that we could measure or map. These were grass community class (as Table 1, below), time since fire (mapped as per methods in paper), estimated number of days since fire where grass had water available to grow (one month after last rain > 5 ml at Mornington), number of days since the start of the dry season (days after April 1st, until December 1st), intensity of fire (high intensity versus mild), and grazing by introduced herbivores (delineated by AWCs destocking fence). For each grass community, we fitted a linear model to every combination of time since fire, fire intensity, dry days, grazing, and an interaction term of time since fire and grazing. Within each grass community, these models were compared within an information theory framework, and the most parsimonious model was determined as that with the lowest AICc and Aikike weight. All analysis was conducted in R (R Development Core Team 2008) using the 'nlme' and 'MuMIn' packages.

Once the most parsimonious model was selected for each grass community, we applied the parameter estimates to each cat fix and associated random fix based on values of predictor variables. We also capped derived values at an upper and lower limit; zero was defined as the lower limit; the upper limit was the average value for the corresponding unburnt plots in each grass communities and grazing type. This allowed us to predict the grass cover, dense grass cover and relative grass biomass at any location within the study area given grass community, time since fire and stocking treatment. All top models had an adjusted R^2 of greater than 0.7.

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Table 1. Parameter estimates used to derive grass cover (%), based on linear models fitted to field measurements for each grass community. Growdays is number of days since fire when grass could grow (one month post rain). Grazing is whether site was stocked with large feral herbivores. Dry months is number of months into dry season (starting April, ending December). Maximum value is the upper limit where values were capped, based on the average grass cover for unburnt plots.

Grass community	Parameter estimates for each grass community						Maximum value	
	intercept	growdays (sqrt)	growdays (sqrt) × grazing?	grazing?	dry months	Early fire	Stocked	Destocked
Riparian forest	8.23	3.78	0	-30	0	15	31	60
Alluvial grasslands	-0.68	5.76	0	-26.35	-6.29	4	75	92
Bluegrass plains	2.49	4.77	0	-29.66	0	5	74	90
Canegrass	5	3.79	0	0	0	0	96	89
Mixed woodlands	7.07	5.08	0	-19.11	-3.37	3	72	91
Sandseep	-17.25	6.93	0	-10.9	-4.53	7	98	96
Hillside woodlands	11.58	3.69	0	0	-15.1	2	80	91
Spinifex woodlands	-0.92	3.75	-0.761	2.54	-2.14	5	70	70
Bare ground	0	0	0	0	0	0		

Appendix 2. Introduction to the footage obtained from the cat video collars

For this appendix, a short video was created. This provides a brief overview of how cameras that were placed on cats were created, along with some of the resultant footage

The video can be accessed via dropbox by the following link:

https://www.dropbox.com/sh/cmtetmmzk59mnm2/AACtlLup-NGVLYLYjik14ONoa?dl=0

If there are any problems viewing this file, please email hughmcgr@gmail.com for assistance